MEMOIRS

of

THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

Number 7

ANT LARVAE: REVIEW AND SYNTHESIS

by

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Published by

THE ENTOMOLOGICAL SOCIETY OF WASHINGTON

Washington, D. C.

1976

Library of Congress Catalog Card Number 76-9334

PRINTED BY:
STORTER PRINTING COMPANY
Gainesville, Florida

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EPIGRAPHS

"An exhaustive monographic study of ant-larvae would certainly repay the investigator, as they present a bewildering array of interesting characters in the various tubercles, 'poils d'accrochage,' etc., with which they are provided."—W. M. Wheeler 1903: 209.

"Aside from those of the saw-flies, the larvae of ants should be more susceptible to taxonomic treatment than those of other Hymenoptera. In general, these do not possess such remarkable modifications as occur in some of the parasitic families, but the characters which they do have are apparently of such nature as to be suitable as a basis for classification."—Brues 1919: 16.

"Largely because of parallelisms, classifications based upon very few characters are often artificial. It follows, then, that the more characters considered in devising a classification, the greater the likelihood that the classification will represent the true phylogeny. It is, therefore, important that systematists search for characters of all sorts, whether they are morphological or bionomic."—Michener 1953a: 117.

"Nevertheless it is an axiom of modern taxonomy that variety of data should be pushed as far as possible toward the limits of practicability. The object of classification should be what Hennig (1950) calls the *holomorph,* all the characteristics of the individual throughout its life."—Simpson 1961: 71.

INTRODUCTION

Ave Atque Vale

With the following discussion of ant larvae in general, our study is temporarily complete. And it is high time, since one of us has reached the ripe age of 78.

We have often referred to our publications on ant larvae as the "monograph." We were facetious, but now that we have totalled the pages and figures, we realize that we might as well have been serious: approximately 850 pages including about 475 figures; this total certainly has the elephantine proportions associated with monographs.

For financial reasons it has been impossible to publish it in "one writing" so it has appeared in 53 papers scattered throughout 12 journals over a period of 45 years, as follows:

American Midland Naturalist (4 papers)
Entomological Society of America, Annals (11)
Entomological Society of America, Bulletin (1)
Entomological Society of Washington, Proceedings (11)
Georgia Entomological Society, Journal (3)
Kansas Entomological Society, Journal (1)
Museum of Comparative Zoology (Harvard), Breviora (1)
Museum of Comparative Zoology (Harvard), Bulletin (1)
Pan-Pacific Entomologist (3)
Psyche (13)
Tennessee Academy of Science, Journal (1)
Washington Academy of Science, Journal (3)

History And Methods

We have already published (1965a) a "History of Myrmecopedology." In 1972b we published a reprint (with translation) of Emery's classic paper "Intorno alle Larve di Alcune Formiche" (1899). "Techniques for the Study of Ant Larvae" appeared in 1960a.

Literature

A complete bibliography of our papers on ant larvae is to be found in Appendix A; we shall cite them hereafter only by the year. There are numerous references to ant larvae by other authors scattered throughout the literature. They range in length from a line to a page. They may concern life cycles, parasites, food, care, etc., but mostly they are descriptive. We have cited all significant references (and some not so significant) that we have been able to find. We are not citing them again but they may be found (if needed) by consulting our papers on the appropriate taxa in Appendix A.

Because of the high cost of publication we have not prepared a unified bibliography of all these references to ant larvae. Such could easily be assembled by combining the literature cited at the ends of all our papers on ant larvae and then eliminating the duplications. We have, of course, our own bibliography in the form of a card index; it comprises 577 cards.

Material Studied

We have studied the larvae of 692 species in 182 genera of ants representing all ten of the living subfamilies. The taxa are given in Appendix

B. A summary by subfamilies of the number of genera and species (in parentheses) follows: Dorylinae 6 (15); Leptanillinae 2 (3); Cerapachyinae 4 (10); Myrmeciinae 1 (30); Ponerinae 42 (138); Pseudomyrmecinae 4 (34); Myrmicinae 83 (264); Aneuretinae 1 (1); Dolichoderinae 13 (53); Formicinae 26 (142).

The specimens studied are now in two collections: microscope slide preparations—2600 slides; larvae preserved in alcohol—560 vials. So far as we know this is the only extensive systematic collection of ant larvae in the world.

Geographical Distribution

This section is a summary of the sources of our material. The figures after each geographical entity represent the number of species from that entity in our collection; the name is usually that used by the collector.

AFRICA—Anglo-Egyptian Sudan 1, Belgian Congo 19, British Cameroons 1, Ghana 4, Ivory Coast 2, Kenya 3, Mauritius 1, Nigeria 1, Rhodesia 4, South Africa 6, Tunis 3. Total 45.

ASIA—Afghanistan 1, Assam 1, Ceylon 2, China 1, Iran 1, India 3, Indo-China 1, Israel 1, Japan 10, Singapore 2, Siam 1, Turkestan 3. Total 27.

AUSTRALIA—ACT 8, New South Wales 111, Northern Territory 2, Queensland 33, South Australia 21, Tasmania 1, Victoria 18, Western Australia 15. Total 209.

CANADA—Manitoba 1.

CENTRAL AMERICA—Canal Zone 45, Costa Rica 22, Guatemala 10, Honduras 2, Panama 21. Total 100.

EUROPE—France 1, Sardinia 1, Siberia 1, Switzerland 5. Total 8.

MALAY ARCHIPELAGO—Borneo 9, Java 9, New Guinea 6, Philippines 22, Sumatra 1. Total 47.

MEXICO—19.

NEW ZEALAND—5.

OCEANIA—Fiji 3, Rarotonga 1, Solomon Islands 6, Society Islands 1. Total 11.

SOUTH AMERICA—Argentina 3, Brazil 38, British Guiana 36, Colombia 6, Ecuador 1, Paraguay 1, Peru 1, Venezuela 2. Total 88.

UNITED STATES—Alabama 4, Arizona 4, Arkansas 2, California 17, Colorado 3, Connecticut 4, Delaware 1, Florida 11, Georgia 9, Illinois 3, Louisiana 4, Massachusetts 6, Michigan 13, Minnesota 1, Mississippi 4, Missouri 1, Montana 2, Nevada 7, New Hampshire 5, New Jersey 4, New Mexico 3, New York 11, North Carolina 1, North Dakota 37, Ohio 1, Oklahoma 9, Oregon 2, South Dakota 1, Texas 28, Virginia 1, Washington 1, West Virginia 1, Wyoming 3. Total 204.

WEST INDIES—Bahamas 3, Cuba 11, Haiti 1, Jamaica 1, Puerto Rico 8, Trinidad 5. Total 29.

MORPHOLOGY

Paradigm For Descriptions Of Ant Larvae

(Unless otherwise specified, a description applies to a *mature worker* larva.)

Length

Shape

Protuberances (if any): abundance; number of types; shape; size; distribution; hairs; spinules

Anus: position; lips (if any)

Leg, wing and gonopod vestiges

Spiracles (if unusual)

Number of differentiated somites

Integumentary spinules: abundance; size; distribution; arrangement

Body hairs: abundance; number of types; shape; length; distribution

Head
- **Size**
- **Shape of cranium in anterior view**
- **Proportions**
- **Integument: spinules or bosses (if any)**
- **Antennae: size; position; shape; sensilla (number, shape)**
- **Hairs: abundance; arrangement; number of types; shape; size**

Labrum
- **Size**
- **Shape**
- **Proportions**
- **Anterior surface: bosses (if any); spinules; hairs; sensilla (number, position)**
- **Ventral border: spinules; sensilla**
- **Posterior surface: sensilla (number and position); spinules (number, size, arrangement)**

Mandibles
- **Size**
- **Sclerotization**
- **Proportions**
- **Shape: general; medial blade; apical tooth (shape, size, direction); medial teeth (number, shape, size, direction)**
- **Spinules (if any): location; size; shape; abundance; arrangement**

Maxillae
- **Size (if unusual)**
- **Shape**
- **Spinules (if any): abundance; location; size; arrangement**
- **Palps: shape; sensilla (number, location, shape)**
- **Galeae: shape; sensilla (number, location, shape)**

Labium
- **Spinules (if any): abundance; location; size; arrangement**
- **Palps: shape; sensilla (number, location, shape)**
- **Isolated sensillum (if any) between each palp and the opening of the sericteries**
- **Opening of sericteries: shape**

Hypopharynx
- **Spinules: abundance, size, arrangement**

SIZE

It was not until 1953 (Pheidolini and Pheidologetini) that we began to give in our descriptions of ant larvae an important datum, namely length. In 1956 (Pseudomyrmecinae) we realized that the length of a straight stiff larva (e.g., Pseudomyrmecinae and Dolichoderinae) is not comparable to the length of a curved flexible larva: the length of the former would be measured from the dorsum of the prothorax to the posterior end of the body, while that of the latter would be from the front of the head to the posterior end (see Fig. 1.). So we began using two measurements on straight larvae: straight length and length through spiracles. Since all our drawings are orthographic projections, the latter measures the length of a line on the drawing from the front of the head through all the spiracles to the anus. This line is also the imaginary long axis of the larva. Furthermore, it can be measured quite easily under a microscope with an eyepiece micrometer.

In most ant larvae only one of these measurements is necessary—length through spiracles. But in those which have the head on the ventral surface—notably the Pseudomyrmecinae and Dolichoderinae—there is considerable difference between the two measurements. For example, in *Leptomyrmex pictus* the straight length is 4.6 mm, but the length through spiracles is 6.4 mm.

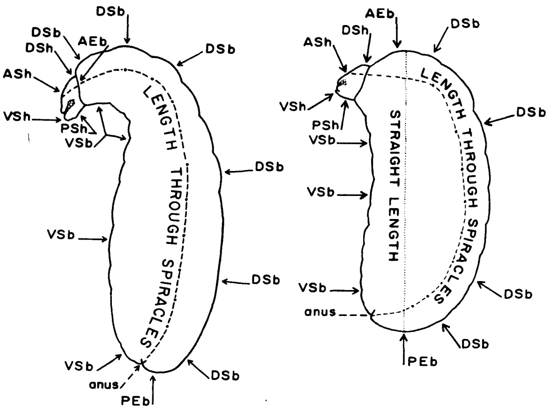

Fig. 1. Measurements and orientation of body. A, anterior; b, body; D, dorsal; E, end; h, head; P, posterior; S, surface; V, ventral.

The largest mature worker larva we have studied is that of *Myrmecia simillima,* which is 35 mm long. Almost as long (34 mm) are the male larvae of *Dorylus wilverthi* and *D. nigricans.* The smallest mature worker larva studied is that of *Leptanilla revelierei sardoa,* which is 1.3 mm long.

COLOR

The typical ant larva is whitish. Perhaps that is why color is so rarely mentioned by authors of descriptions. Where color has been mentioned at all it has usually been white or some nearly white shade:—*Dorylus affinis* "bianchissime," *Eusphinctus steinheili* dull white, *Dolichoderus bituberculatus* opaque white, *Iridomyrmex humilis* pure white, *Myrmecia sanguinea* milk white, *Paranomopone relicta* pure white, *Paraponera clavata* blue white, *Diacamma rugosum geometricum* white, *Megaponera foetens* grayish white, *Myrmica brevinodis canadensis* pearly white, *Stenamma westwoodi* grayish white, *Aphaenogaster simonellii* dirty white, *Pheidole pallidula arenarum* whitish, *Monomorium pharaonis* white, *Solenopsis molesta* white, *Paedalgus termitolestes* white, *Myrmecina graminicola* (young) white, *Tetramorium caespitum* (young) white, gleaming white, *Leptothorax rottenbergi semiruber* whitish, *Plagiolepis longipes* (young) glassy white, *Lasius alienus americanus* white, *Oecophylla smaragdina virescens* milk-white, *Camponotus (Tanaemyrmex) aethiops concava* whitish, *C. (T.) ae. andria* whitish.

In frequency yellowish is next:—*Tapinoma sessile* yellowish, *Simopelta pergandei* cream, *Monomorium algiricus* (young) yellowish, *Myrmecina graminicola* (mature) yellowish, *Tetramorium caespitum* (mature)

yellowish white or yellow, genus *Leptothorax* whitish yellow, *Harpagoxenus americanus* (young) yellowish, *Pogonomyrmex barbatus* cream-colored, genus *Myrmica* yellow, genus *Lasius* pale yellowish white, genus *Formica* pale yellowish white.

Gray has been reported rarely:—*Bothroponera sublaevis* "a peculiar opaque, gray color," *Anergates atratulus* "a peculiar gray color," *Plagiolepis longipes* (mature) grayish.

Green has been mentioned only once:—*Myrmica brevinodis* var. *sulcinodoides*, a pecular greenish-yellow color and oily luster.

In our recent field notes we have recorded the following observations on color. *Manica bradleyi*: the larvae may be white, creamy white or greenish; semipupae and pupae may be white, yellow, salmon or orange. *Iridomyrmex pruinosus*: salmon or orange. *Dorymyrmex pyramicus*: pale yellow or greenish. *Myrmecocystus mexicanus*: large larvae are greenish yellow; sexual larvae are yellow. *Formica obtusopilosa*: larvae grayish; semipupae and pupae yellowish.

We have rarely mentioned color in our descriptions, partly because most of our material has been preserved and well preserved larvae are invariably whitish, and partly because most of the living larvae we have seen are likewise whitish. Furthermore we have found that the color of larvae of the same species in the same nest may vary somewhat; also we suspect the color of the same larva may change with age or other conditions. For *Manica* we have noted (1970: 145) that "larvae are often creamy white with a dirty gray meconium showing through from interior; becoming yellowish, especially at the anterior end; semipupae and pupae usually yellow; but brood of same size may be white, yellow or orange."

Young larvae are often partly transparent. Small scattered white patches show through the integument; they are said to be urate crystals. As the larva grows the space between the organs becomes filled with lobes of the voluminous fat body, which give the larva its definitive color. All internal tissues are sufficiently translucent in older larvae to allow the dark-colored meconium to show through.

The mandibles of ant larvae are usually darker than the body, ranging from light amber to dark brown depending upon the degree of sclerotization, the darkness varying directly with the hardness.

BODY SHAPE

We have studied the larvae of 182 genera of ants representing all 10 living subfamilies and 47 of the 60 tribes. (The tribes not represented are all monotypic and rare.) Deducting those genera represented only by immatures, damaged material, or semipupae, we have in our collection mature larvae of 158 genera of ants.

With few exceptions, every genus has its own distinct body-shape. Not unexpectedly, then, we have found body-shape to be the most useful taxonomic character for larvae. In our comparisons of body shapes we have used only the profiles (Fig. 2) (i.e., bare outlines in left side view), since dorsal and ventral views rarely show anything distinctive. Our technique for comparing profiles has been explained in 1960c: 101-104.

Now 158 profiles is an unmanageable number for simultaneous comparison, but by means of our technique we were able to arrange them in 38 groups of somewhat similar profile. We designated each by a name derived from the name of an included genus plus the Latin suffix *-form.*

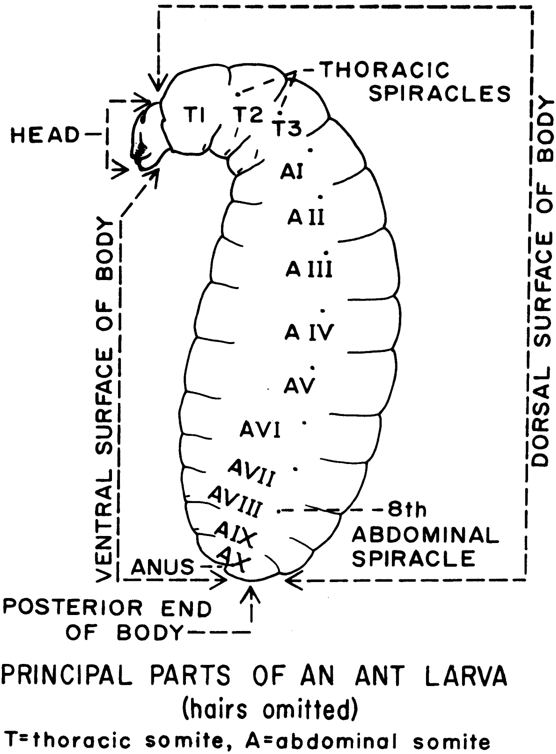

Fig. 2. Hypothetical generalized body in side view.

So far we had stayed within subfamilies (Dorylinae 1964a, Cerapachyinae 1964b, Ponerinae 1964c, Myrmicinae 1960c, Dolichoderinae 1966, Formicinae 1970b), but when we crossed boundaries, we found many intersubfamilial resemblances. So we shuffled profiles among subfamilies,

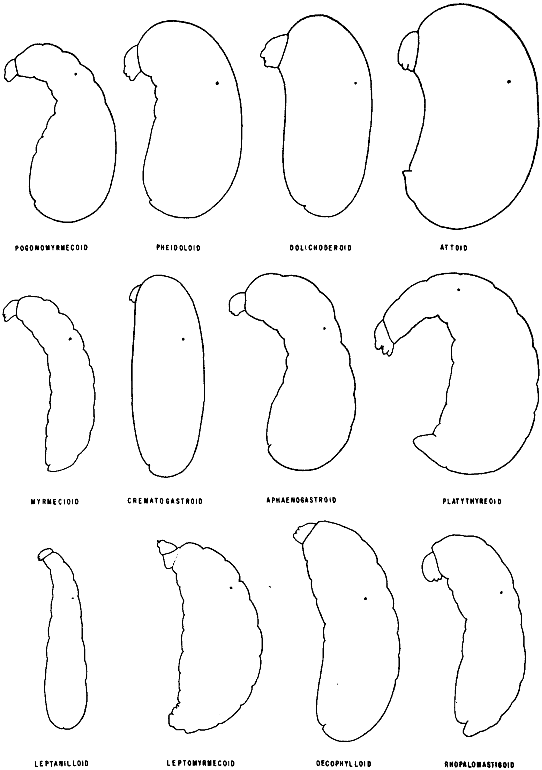

Fig. 3. Classification of body profiles. For explanation see text.

and finally, after all this legerdemain, we ended up with 31 profiles for the family Formicidae. This was still too many; so we made a third approximation and ended up with 12 types, which are described in the following list and illustrated in Fig. 3. This number should be manageable. To

avoid confusion with the profile-types within the subfamilies, we have given to these family profile-types names based upon an included genus plus the Greek *-oid*, meaning "like."

1. POGONOMYRMECOID—Diameter greatest near middle of abdomen, decreasing gradually toward head and more rapidly toward posterior end, which is rounded; thorax more slender than abdomen and forming a neck, which is curved ventrally. Occurrence:—PONERINAE: *Amblyopone, Anochetus, Belonopelta, Bothroponera, Brachyponera, Centromyrmex, Cryptopone, Diacamma, Dinoponera, Ectatomma, Euponera, Gnamptogenys, Heteroponera, Hypoponera, Leptogenys, Mesoponera, Myopias, Neoponera, Odontomachus, Odontoponera, Ophthalmopone, Pachycondyla, Paraponera, Ponera, Psalidomyrmex, Rhytidoponera, Stigmatomma, Trapeziopelta.* MYRMICINAE: *Clarkistruma, Colobostruma, Daceton, Dacryon, Dilobocondyla, Epopostruma, Eurhopalothrix, Leptothorax (Mychothorax* and *Nesomyrmex), Liomyrmex, Manica, Messor, Myrmecina, Myrmica, Orectognathus, Paramyrmica, Podomyrma, Pogonomyrmex, Pristomyrmex, Tetramorium.* FORMICINAE: *Acanthomyops, Camponotus, Diodontolepis, Echinopla, Formica, Gesomyrmex, Gigantiops, Lasius, Melophorus, Myrmecocystus, Myrmecorhynchus, Notoncus, Opisthopsis, Plagiolepis, Polyergus, Polyrachis, Prolasius.*

2. PHEIDOLOID—Abdomen short, stout and straight; head ventral near anterior end, mounted on short stout neck, which is the prothorax; ends rounded, one end more so than the other. Occurrence:—MYRMICINAE: *Allomerus, Anergates, Calyptomyrmex, Cardiocondyla, Carebara, Chelaner, Lophomyrmex, Machomyrma, Macromischoides, Mayriella, Megalomyrmex, Meranoplus, Monomorium, Myrmicaria, Oligomyrmex, Oxyepoecus, Paedalgus, Pheidole, Pheidologeton, Rogeria, Smithistruma, Solenopsis, Strumigenys, Vollenhovia, Wasmannia.* DOLICHODERINAE: *Engramma.* FORMICINAE: *Brachymyrmex, Stigmacros.*

3. DOLICHODEROID—Short, stout, plump, straight or slightly curved, with both ends broadly rounded; anterior end formed by enlarged dorsum of prothorax; head ventral, near anterior end; no neck; somites indistinct. Occurrence:—DOLICHODERINAE: *Araucomyrmex, Bothriomyrmex, Dolichoderus, Dorymyrmex, Forelius, Froggattella, Iridomyrmex, Tapinoma.* FORMICINAE: *Paratrechina.*

4. ATTOID—Similar to dolichoderoid but shorter, stouter and more curved; diameter approximately equal to distance from labium to anus, whereas in dolichoderoid it is about half that distance. Occurence:—MYRMICINAE (Tribe Attini): *Acromyrmex, Apterostigma, Atta, Cyphomyrmex, Mycetosoritis, Myrmicocrypta, Sericomyrmex, Trachymyrmex.*

5. MYRMECIOID—Elongate and rather slender; curved ventrally; without a differentiated neck; diameter diminishing only slightly from fifth abdominal somite to anterior end. Occurrence:—MYRMECIINAE: *Myrmecia.* PONERINAE: *Megaponera, Myopopone, Prionopelta.* DORYLINAE: *Aenictus, Cheliomyrmex, Dorylus, Eciton, Labidus, Neivamyrmex.* CERAPACHYINAE: *Cerapachys, Eusphinctus, Lioponera, Phyracaces.*

6. CREMATOGASTROID—Elongate-subelliptical; head applied to ventral surface near anterior end; no neck; somites indistinct. Occurrence:—PSEUDOMYRMECINAE: *Pachysima, Pseudomyrmex, Tetraponera, Viticicola.* MYRMICINAE: *Cataulacus, Cephalotes, Crematogaster, Cryptocerus, Leptothorax (L.* and *Dichothorax), Macromischa, Procryptocerus, Xenomyrmex.* DOLICHODERINAE: *Azteca.* FORMICINAE: *Myrmelachista.*

7. APHAENOGASTROID—Slightly constricted at first abdominal somite, diameter increasing gradually toward middle of thorax and of abdomen; thorax arched ventrally but not forming a distinct neck; posterior end broadly rounded. Occurrence:—PONERINAE: *Onychomyrmex, Typhlomyrmex.* MYRMICINAE: ~~*Acanthognathus,*~~ *Alistruma, Aphaenogaster, Aspididris, Mesostruma, Novomessor, Ocymyrmex, Rhopalothrix, Stenamma, Veromessor.* FORMICINAE: *Prenolepis.*

8. PLATYTHREOID—Both ends directed ventrally from a straight body; terminal somite taillike. Occurrence:—PONERINAE: *Discothyrea, Eubothroponera, Platythyrea, Proceratium.*

9. LEPTANILLOID—Elongate, slender and club-shaped. Occurrence:—LEPTANILLINAE: *Leptanilla, Leptomesites.* PONERINAE: *Apomyrma.* MYRMICINAE: *Trigonogaster.*

10. LEPTOMYRMECOID—Elongate, stout and slightly curved; diameter greatest at third and fourth abdominal somites, decreasing rapidly toward either end; 3 posterior somites small and directed ventrally; prothorax sharply differentiated into 2

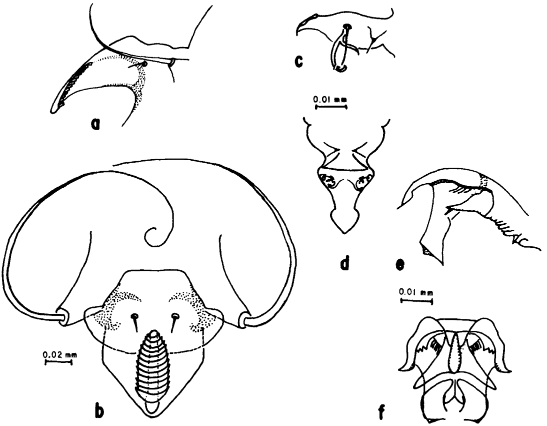

Fig. 4. Leptanilline protuberances. *Leptomesites escheri*, a and b: a, side view; b, anterior view. *Leptanilla revelierei sardoa*, c and d: c, side view; d, anterior view. *Leptanilla swani*, e and f: e, side view; f, anterior view.

parts, the anterior wedge-shaped (longer below) and abruptly depressed below posterior part; head on anterior end with mouth parts directed anteriorly; somites distinct. Occurrence—DOLICHODERINAE: *Leptomyrmex*.

11. OECOPHYLLOID—Plump, sausage-shaped, slightly curved; diameter nearly uniform; no neck; head on anterior end. Occurrence:—FORMICINAE: *Oecophylla*.

12. RHOPALOMASTIGOID—Diameter nearly uniform; slightly constricted between first and second abdominal somites; body bent ventrally from this constriction; terminating posteriorly in a conspicuous knob; head ventral, near anterior end. Occurrence:—MYRMICINAE: *Rhopalomastix*.

PROTUBERANCES

The body outlines of a conventional ant larva are smooth except for the more-or-less marked indentations due to the intersegmental grooves. Nevertheless in 41 out of the 182 genera studied we have found that something has been added—some sort of protuberance from the conventional outline; see Fig. 5. These protuberances we divide for convenience into three groups:

(1) The leptanilline protuberance (see Fig. 4), for which we have not yet thought of a suitable name.

(2) Welts. We use this term when the protuberance is low, elongate and narrow.

(3) Tubercles. All other shapes, including what we have usually termed bosses, if they are low, convex and subcircular. We have already discussed tubercles at some length (1964c, 1966, 1971b).

The term "tubercle" is not particularly appropriate for these structures. The Latin *tuberculum* is the diminutive of *tuber*, which means swelling, hump, bulb, bump, or protuberance. Definitions in English dictionaries employ such nouns as "excrescence," "protuberance," and "nodule," modified by the adjectives "round," "rounded" or "knoblike." But not many ponerine tubercles can qualify for roundness. Torre-Bueno's "Glossary of Entomology," however, defines tubercle as "a little solid pimple or small button." A pimple is pointed and a button may be knoblike. Seemingly, then, entomological usage takes care of all types of ponerine tubercles. Nevertheless the definition must be stretched to the breaking-point (or beyond) to include the spinelike tubercles of *Centromyrmex* and the "pulleys" of *Anochetus*. Be that as it may, myrmecological usage definitely sanctions the term. In 1886 Müller used *Tuberkeln* when referring (in German) to the rounded protuberances of mature *Pachycondyla* larvae; the conical structures on the young larvae were merely *Erhebungen*. Emery in 1899 used *sporgenze segmentali o tubercoli del tegumento* when referring in Italian to both rounded and pointed projections in 3 genera. In the "Genera Insectorum" (1911) he used the French *tubercules*. Wheeler first used "tubercles" in 1900 in "A Study of Some Texan Ponerinae" (his second article on ants) and he was still using it in 1922. In German Eidmann used *Warzen, Dörnchen, Fortsätze, Auswüchse* and *Höcker*.

We shall next consider the taxonomic occurrence of protuberances.

LEPTANILLINAE—The larvae of the two genera (*Leptanilla* and *Leptomesites*) have a curious complex structure projecting anteroventrally from the ventral surface of the prothorax. An examination of our fig. 4 will show why we have neither named nor described it. We do, nevertheless, consider it a subfamilial character.

CERAPACHYINAE—In *Phyracaces elegans* there is a boss on the ventrolateral surface of each AI-AVI. *Cerapachys australis* has a small posteriorly projecting boss on AX.

PONERINAE—In the "Genera Insectorum" Emery (1911: 4) divided the subfamily Ponerinae into 3 sections on the basis of larval and male characters. Section Prodorylinae is practically equivalent to the present subfamily Cerapachyinae and hence can be disregarded in this discussion. In section Proponerinae the larvae were characterized as *uniformément poilues, sans tubercules piligères*, while those in section Euponerinae were *pourvues de tubercules piligères*.

This division is of historical interest: it is Emery's second use of larval characters in formicid taxonomy. But is it still valid and useful? It is not particularly useful, since tribes adequately take care of the interval between subfamily and genus. It is valid only if a few exceptions are allowed. Without knowing either the larvae or most males, Emery placed *Discothyrea, Platythyrea, Proceratium* and *Thaumatomyrmex* in the Proponerinae and *Onychomyrmex* in the Euponerinae; he had seen the male but not the larva of *Megaponera*, which he placed in the Euponerinae. We now know that the larvae of *Discothyrea, Eubothroponera, Platythyrea, Proceratium* and *Thaumatomyrmex* have tubercles while those of *Megaponera* and *Onychomyrmex* lack them.

Furthermore not all tubercles are piligerous. To be sure, those without obvious hairs usually have one or more sensilla, each of which may

bear a spinule or minute hairlike structure, but we are not willing to dignify them with the term "hair" (although we have done so in the past).

We have described (1952a, 1964c, 1971b) the protuberances of mature larvae of 27 genera of Ponerinae:

Tribe Platythyreini. *Eubothroponera, Platythyrea.* Transverse welts and paired tubercles on the ventral surface.

Tribe Proceratiini. In *Proceratium* the surface is thickly beset with large hemispherical bosses. In *Discothyrea* we have found one pair of ventrolateral bosses on the prothorax in the species *antarctica*, but none on an unnamed species (1971b: 1203).

Tribe Ponerini. *Belonopelta, Bothroponera, Brachyponera, Centromyrmex, Cryptopone, Diacamma, Dinoponera, Euponera, Hagensia, Hypoponera, Leptogenys, Mesoponera, Myopias, Neoponera, Odontoponera, Ophthalmopone, Pachycondyla, Ponera, Psalidomyrmex, Trapeziopelta.* The only known genus in the tribe that lacks tubercles is *Megaponera.*

Tribe Thaumatomyrmecini. *Thaumatomyrmex.*

Tribe Odontomachini. *Anochetus, Odontomachus.*

In general a ponerine larva bears protuberances of only 1 kind, but 2 distinct kinds are found in 9 genera (*Anochetus, Belonopelta, Bothroponera* Type II, *Cryptopone, Euponera, Hypoponera, Myopias, Odontomachus* and *Ponera*) ; *Brachyponera* has 3 kinds. The number of tubercles per larva seems to be a generic characteristic, although it does vary within narrow limits among the species of a genus and even among individuals of the same species. The minimum number is 2 (*Discothyrea antarctica*) and the maximum about 600 (*Hagensia*), but the count for most genera lies between 100 and 200. The arrangement of tubercles usually follows a simple but definite pattern of longitudinal and transverse rows. No tubercles have been found on the mid-ventral surface except in *Platythyrea.*

We have endeavored to classify and name the various shapes of ponerine tubercles and to illustrate each shape with a synthetic drawing (see Fig. 5). Only fully developed tubercles have been considered. One finds atypical tubercles on every larva, but they are obviously underdeveloped representatives of the typical form.

PSEUDOMYRMECINAE—The trophothylax, or feed-bag, which is distinctive for this subfamily, is formed from the depressed ventral surfaces of the thorax and AI, a welt from the ventral surface of AII and paired ventrolateral bosses on T1, T2 and T3. For details see 1956a. In *Pachysima* the first stage larvae have elaborate tentaclelike and leglike structures which are reduced as the larvae mature. In *P. aethiops* the midventral tentaclelike projection is reduced in the mature larva to a digitiform projection. (See W. M. Wheeler 1918; G. C. and J. Wheeler 1956a.)

MYRMICINAE—In view of the fact that this is the largest subfamily of Formicidae it is indeed surprising that we have found protuberances in only a few genera (*Crematogaster, Leptothorax, Rhopalomastix* and *Dacetinops*) of the 80 represented in our collection.

In *Crematogaster lineolata* Type B we reported (1952c) that "the thoracic somites and the first seven or eight abdominal somites bear each a pair of conspicuous lateral welts; each welt elongate dorsoventrally and narrow anteroposteriorly; it stains deeply with acid fuchsin and its surface is rugose."

The paired lateral projections on the larva of *Crematogaster rivai luctuosa* Menozzi (1952c after Menozzi) and on the larva of *Crematogaster scutellaris* Olivier (1952c after Eidmann) should probably be considered as tubercles.

The pair of ventrolateral bosses on the prothorax in *Leptothorax* (*Mychothorax* and *Nesomyrmex*) (1955b) are also considered protuberances.

In *Rhopalomastix* there is a single posterodorsal boss.

In *Dacetinops* (immature) AII and AIII each has a transverse ventral welt.

ANEURETINAE—In our immature larva of *Aneuretus* (1956c) the terminal portion of the tenth abdominal somite is produced into a naked knob.

DOLICHODERINAE—Except that they are all protuberances, dolichoderine tubercles (1951, 1966) have little in common with ponerine (1964c), differing in several respects:—(1) In number. Among the Ponerinae the number of tubercles per larva ranges between 2 and 600, although the count for most genera lies between 100 and 200. Among the Dolichoderinae the number ranges from 1 to 8. (2) In position. In the Ponerinae the tubercles are generally distributed over the dorsal and lateral surfaces, while dolichoderine tubercles have been found only at or near the posterior end or on the dorsal surface or on the ventral surface of the prothorax. (See fig. 5 XI.) (3) In shape. Although ponerine tubercles vary greatly in form, the majority are either spinelike or bear stout hairs, and could conceivably serve a defensive function. Dolichoderine tubercles lack hairs, are never spinelike and, for the most part, are smoothly rounded.

The following list summarizes the tubercles we have found in the subfamily Dolichoderinae. The structures are most conspicuous in young larvae, but since they remain the same in size they become relatively smaller and therefore less conspicuous as the larva grows.

Dolichoderus. A pair of ventrolateral bosses frequently present.

Dorymyrmex. A slender subconical tubercle at the posterior end.

Forelius. A middorsal boss on the second abdominal somite.

Iridomyrmex. 1-5 rounded bosses (1 per somite) along the middorsal line.

Azteca. Prothorax with a pair of ventrolateral bosses.

Bothriomyrmex. Prothorax with a pair of anteroventral bosses. In the young larva of one species (1951) each boss is produced into a fingerlike projection.

Engramma. Paired dorsal bosses, which are more prominent anteriorly, and a conspicuous knob at the posterior end.

Tapinoma. A rounded posterodorsal boss.

Technomyrmex. A rounded posterodorsal boss.

FORMICINAE. In the tribe Formicini the posterior and lateral walls of the praesaepium are formed by welts. See 1953d: 180.

OTHER SUBFAMILIES—We have found no protuberances in the subfamilies Dorylinae and Myrmeciinae.

Of what use are these protuberances? Not a great deal is really known, but five functions have been suggested:

1. Support. The customary resting position for ponerine larvae is on the side; the usual feeding position is ventral surface up. In either position the tubercles (which are largely confined to the lateral and dorsal surfaces) might prove beneficial by keeping most of the body surface away from the substrate. It is difficult to see any advantage in this in temperate zones, because ants can move their brood to those nest chambers which have a suitable humidity. In the tropics, however, soil moisture may be so high that optimal conditions cannot be found; hence an airspace between body and substrate might be beneficial. At any rate, the Ponerinae are largely tropical.

2. Defense. Probably the greatest menace to a ponerine larva is her sister larvae. It is easy to believe that some of the hairy tubercles afford protection against cannibalism. Emery (1899 and our 1972b: 4) reported an instance of defense in the larvae of *Mesoponera stigma* (Fabricius) as observed by Biró: "In the galleries of the nest excavated in the rotten wood, were found the long-necked larvae, covered with peculiar spines: abandoned by their cowardly custodians, the larvae were able to defend themselves; when any termites. . .approached one of them, the larva beat back and forth with its swan-neck and was soon left in peace."

3. Attachments to ceilings and walls. This is certainly probable in the case of the glutinous dorsal doorknobs; at least attachment can be readily observed in artificial formicaries. It would keep the larvae off the damp floors. (See 1 above.)

4. Trophallaxis. It has been suggested by W. M. Wheeler (1918) and others that tubercles may be exudate organs, which secrete onto their surfaces substances of which the workers are so fond that they tend the larvae for the "selfish" purpose of getting these exudates.

5. Holding food. The trophothylax of the Pseudomyrmecinae is enclosed by bosses and a welt. See 1956a. The similar (but simpler) praesaepium of the tribe Formicini (in the Formicinae) is bordered by welts. See 1953d; 180, 189 and 1970b: 650.

Below we give our classification of protuberances according to shape for the entire family Formicidae together with names of the taxa in which each shape occurs. These are illustrated in Fig. 5.

I. SUBCONE

Subconical, varying from very slender (spirelike or digitiform) to stout; with or without a few lateral hairs; apex with or without 1-3 sensilla or hairs.

a. Slender (i.e., spirelike or digitiform). PONERINAE—*Belonopelta, Bothroponera piliventris, Cryptopone, Hypoponera, Mesoponera australis, M. caffraria, M. melanaria, M. wroughtoni, Myopias, Neoponera, Odontoponera, Ophthalmopone, Ponera, Thaumatomyrmex* and *Trapeziopelta.*

b. Stout. PONERINAE—*Bothroponera denticulata, B. lutea, B. sjostedti, B. sublaevis, Brachyponera, Leptogenys, Mesoponera constricta, M. fauveli, M. gilberti, M. melanaria* and *Neoponera moesta.*

c. Frustum with an apical hair (which is sometimes capitate). PONERINAE—*Bothroponera mayri.*

d. Multiple subcones, each with an apical sensillum or minute hair. PONERINAE—*Bothroponera mayri.*

e. Skewed subcone, with one or more basal hairs. PONERINAE—*Myopias.*

II. SPINE

Spinelike, very slender; base expanded, with or without two long fine flexuous basal hairs; similar to slender subcone but without apical sensilla or hairs. PONERINAE—*Centromyrmex, Euponera, Hagensia, Psalidomyrmex.*

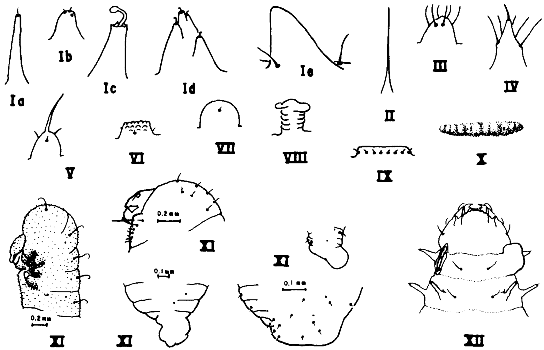

Fig. 5. Classification of protuberances. For explanation see text.

III. CONOID

Conoidal, with an apical nipple (=mammiform); with or without 4-10 long simple slightly curved basal or lateral hairs. PONERINAE—*Dinoponera, Pachycondyla, Probolomyrmex angusticeps* (Taylor 1965: 348-349).

IV. FRUSTUM WITH SPIRE

A frustum surmounted by a spire; frustum with 1-14 long simple slender slightly curved hairs; apex with a heavy straight spinelike hair. PONERINAE—*Anochetus, Odontomachus.*

V. CONOID WITH SPINE

A conoidal base produced into a long slender curved spine; conoid with 1-6 simple hairs. PONERINAE—*Bothroponera cariosa, Diacamma rugosum, D. scalpratum.*

VI. ROUNDED FRUSTUM

A rounded frustum; with two small hairs near the base; apex with numerous minute conoidal papillae. PONERINAE—*Diacamma australe.*

VII. HEMISPHERE

Hemispherical, a few sensilla or minute hairs present. PONERINAE—*Proceratium.*

VIII. DOORKNOB

Mushroom-shaped; cap may have two sensilla. Limited to the dorsal surface of certain abdominal somites, a pair on each. PONERINAE—*Belonopelta, Brachyponera lutea, Cryptopone, Hypoponera, Myopias, Ponera, Simopelta* (immature).

IX. DISCOID

Glabrous subcircular areas which may be considerably elevated and pulleylike or thin discs or merely differentiated areas which are scarcely perceptible in profile; limited to the dorsal surface of abdominal somites IV and V, one or a pair on each. PONERINAE—*Anochetus, Brachyponera sennaarensis, Mesoponera australis, Odontomachus.*

X. WELT

An elongate rounded slightly raised protuberance. PONERINAE—*Eubothroponera, Platythyrea, Probolomyrmex angusticeps* (Taylor 1965: 348); PSEUDOMYRMECINAE;

MYRMICINAE—*Crematogaster lineolata* type B, and *Dacetinops cibdela* (immature); DOLICHODERINAE—*Bothriomyrmex, Engramma lujae* (immature); FORMICINAE—Camponotini (except *Echinopla*), *Formica, Gesomyrmex kalshoveni, Lasius, Polyergus, Prenolepis.*

XI. BOSSES

A boss is an elevated structure with a rounded terminus. PONERINAE—*Discothyrea antarctica, Eubothroponea, Platythyrea, Simopelta* (immature); PSEUDOMYRMECINAE; ANEURETINAE—*Aneuretus* (immature); DOLICHODERINAE—*Araucomyrmex, Azteca, Bothriomyrmex, Dolichoderus, Dorymyrmex, Engramma, Froggattella, Iridomyrmex, Leptomyrmex, Tapinoma, Technomyrmex*; MYRMICINAE—*Cataulacus taprobanae, Crematogaster rivai* (Menozzi 1930), *C. scutellaris* (Berlese 1902), *Leptothorax* (*Mychothorax* and *Nesomyrmex*), *Rhopalomastix*; FORMICINAE—tribe Formicini.

XII. FLAP

A thin rounded flap (a pair on the ventrolateral surfaces of the prothorax). PONERINAE—*Hypoponera* "sp. N. S. W." (1952a: 634).

XIII. TENTACLELIKE

Base pear-shaped, extending into a "slender, apparently erectile, tentacle-like process which . . . terminates in a small ampulla" (W. M. Wheeler 1918: 305). PSEUDOMYRMECINAE—*Pachysima aethiops* (first stage larva). [Not illustrated here. See our 1956a.]

XIV. LEGLIKE

Base swollen and fusiform, extending into a slender stalk, angled and slightly swollen apically (W. M. Wheeler 1918: 309). PSEUDOMYRMECINAE—*Pachysima latifrons* (first stage larva). [Not illustrated here. See our 1956a.]

XV. CONE-SHAPED WITH NARROW NECK

"A low cone-shaped structure articulated to the terminal somite by a narrow neck (in life the flat base of the cone serves to attach the larva to the ceiling or walls of the nest)" (Taylor 1965: 348). PONERINAE—*Probolomyrmex angusticeps.* [Not illustrated here.]

ANUS

The anus of an ant larva is a transverse slit located on the tenth somite, slightly ventral to the posterior end of the body. This position we have called posteroventral or subterminal (41% of the genera). Due to differential development of various parts of the posterior somites the anus may appear (at least in preserved material) on the ventral surface near the apparent posterior end; this position we have called ventral. It is the position most frequently found. Rarely (13 genera) the anus is on the apparent posterior end; this position we have called terminal.

The differences between posterior and posteroventral and between posteroventral and ventral are sometimes difficult to determine in preserved material (even more difficult in living specimens) on a curve without basic points of reference and there is always the possibility that the difference may be artifactual. In some groups, however, the position of the anus does seem to be a moderately good taxonomic character at the generic level.

The ventral position seems to be weakly correlated with greater specialization in other characters.

Sometimes the anus is furnished with lips, which are also moderately useful characters. In seven genera there are two lips, anterior and posterior: *Acanthomyops, Apomyrma, Apterostigma, Dolichoderus, Lasius, Myrmecocystus, Myrmicocrypta.* The posterior lip is always the larger. In 22 genera there is only the posterior lip.

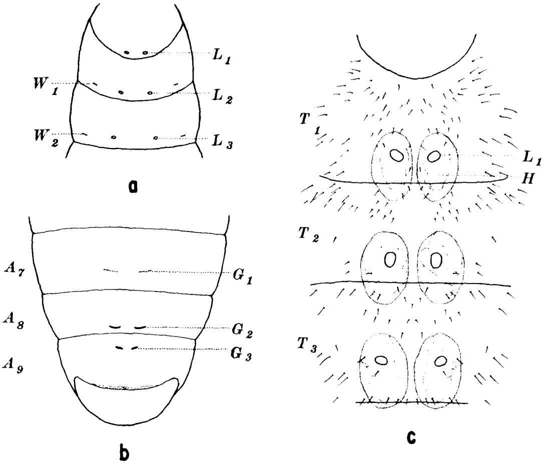

Fig. 6. Leg and gonopod vestiges and wing rudiments. a, thoracic somites in ventral view (*Neivamyrmex schmitti* male) showing positions of leg vestiges (L_{1-3}) and wing rudiments ($W_{1,2}$); b, posterior end (A_{7-10}) of body in ventral view (*Pseudomyrmex gracilis*) showing gonopod vestiges (G_{1-3}); c, thoracic somites (T_{1-3}) in ventral view (*Eciton hamatum*) showing leg vestiges and their position in relation to underlying developing leg buds of mature ant (e. g., L_1 and H). (After G. C. Wheeler, 1938.)

VESTIGES

In 1938 G. C. Wheeler described and discussed certain structures which he had found to be of general occurrence among ant larvae and which he named "leg vestiges", "gonopod vestiges" and "wing rudiments." We have little to add to that discussion.

Leg vestiges are almost universal among ant larvae; we have found them in all subfamilies except the aberrant Leptanillinae. Even in those genera where we have been unable to find them, we have never been sure that our failure might not be due to small size or defective material.

Leg vestiges (Fig. 6 and 7) are to be found in pairs, one pair on the ventral surface of each thoracic somite near its posterior border. They are most conspicuous in the Dorylinae, Myrmeciinae and Ponerinae, where they often have the form of subcircular, convex, slightly elevated papillae. In other subfamilies they more commonly appear as short transverse lines (grooves or ridges?), which are difficult to see.

Gonopod vestiges likewise occur in pairs, one pair on the ventral surface of one or more abdominal somites VII, VIII and IX. In some genera

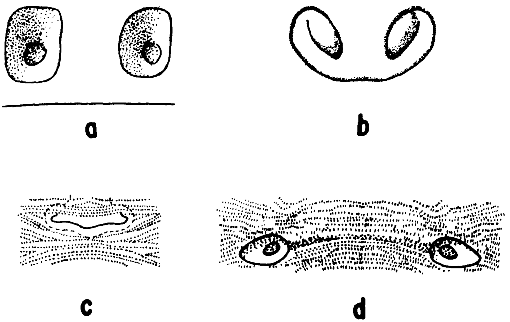

Fig. 7. a, Prothoracic leg vestiges of *Bothroponera sublaevis*; b, mesothoracic leg vestiges of *Myrmecia gulosa*; c, metathoracic leg vestiges of *Megaponera foetens*; d, metathoracic leg vestiges of *Bothroponera sublaevis*.

they are papillose, but as a rule they appear as short transverse lines (slits?).

"On the mesothorax and metathorax there are small paired structures—probably grooves—located one on each side approximately midway between the leg vestige and the spiracle, i.e., ventrolateral and therefore in close proximity to the imaginal buds of the wings. These can hardly be termed wing vestiges, since there is no reason for assuming that the ancestral larva had functional wings. They may, however, be vestiges of wing-pads of the nymph of a heterometabolous ancestor. Finally they may be prothetelous, i.e., adult structures appearing prematurely in the larva. I shall call them provisionally 'wing rudiments.'" (G. C. Wheeler 1938: 140-141.) Wing rudiments are less common than leg vestiges or gonopod vestiges.

In one species, *Crematogaster lineolata subopaca* Emery Type B (1952c), we have found abdominal leg vestiges (?) on somites I-III. They are much more conspicuous than those on the thorax; in alcoholic material they are brown and can be readily seen at a low magnification. Typically three pairs are present, but the number may vary from zero to six.

SEGMENTATION

An ant larva consists of a head and 13 somites. The first three somites will become the thorax of the adult (we have symbolized them by T1, T2 and T3), the fourth (AI) will become the epinotum, the fifth (AII) the petiole, the sixth (AIII) either the postpetiole or the first gastric somite and the sixth (AIII) or seventh (AIV) through the thirteenth (AX) the gaster.

It is not always possible to distinguish all 13 somites. Even when the anterior somites are distinct, some of those at the posterior end may not

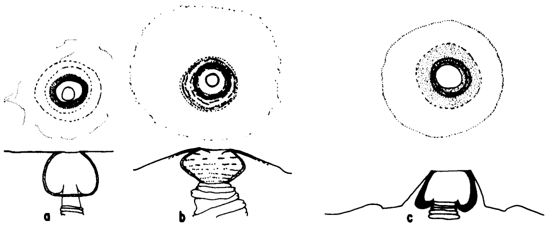

Fig. 8. Spiracles. Upper row, surface view; lower row, optical section. a, Narrow peritreme, large atrial opening, simple atrial wall, small tracheal opening; b, opening on slight elevation, wide peritreme, atrial opening narrow, atrial wall with simple spinules in short rows, tracheal opening wider; c, opening of spiracle on papilla, atrial opening wide, atrial wall heavily sclerotized but without spinules, tracheal opening slightly narrower. (a, *Odontoponera transversa,* X339; b, *Myrmecia gulosa,* X185; c, *Paraponera clavata,* X267.)

be differentiated. In larvae with the dolichoderoid, attoid and crematogastroid profiles it may be difficult or impossible to see any segmentation.

SPIRACLES

A typical ant larva has ten pairs of spiracles, a pair each on the mesothorax, metathorax and eight anterior abdominal somites; certain dolichoderines have nine pairs; Leptanillinae have only one pair, which is on AIII. In about half the genera studied the spiracles are small and of uniform size; in the remainder either one or more of the three anterior pairs are greater in diameter or the spiracles decrease progressively posteriorly. All are large enough, however, to reveal something more than a hole and to show some differences within the family.

We did not recognize these differences, however, until quite recently. On restudying our material we found that 130 genera had spiracles with an unadorned atrium as in Fig. 8a. These resemble the spiracles of the wasp larva *Pemphredon tenax* Fox (Evans 1958 pl. VII fig. 52). This simple type of spiracle occurs in 24 genera of Ponerinae and 56 of Myrmicinae, in all Dorylinae, Cerapachyinae, Pseudomyrmecinae, Aneuretinae and Dolichoderinae and all but one genus of Formicinae. We found other spiracles with simple minute spinules on the inner surface of the atrium (see Fig. 8b). These resemble the spiracles of the wasp larva *Sphecius speciosus* (Drury) (Evans and Lin 1956 pl. V. fig. 36). They are found in all species of Myrmeciinae, in 14 genera in Ponerinae, 19 in Myrmicinae and 6 in Formicinae. A third type occurs in two ponerine genera, *Paraponera* and *Thaumatomyrmex,* in which each spiracle is in a peg set in a slight depression (Fig. 8c).

Either of the first two types is distributed along the body of a larva or both types occur in a regular pattern on each larva, or in a genus some species lack spinules and some have spinules in all or some of the spiracles.

The spiracular peritreme may be absent or present and when present, ranges from feebly to strongly sclerotized. The opening into the trachea

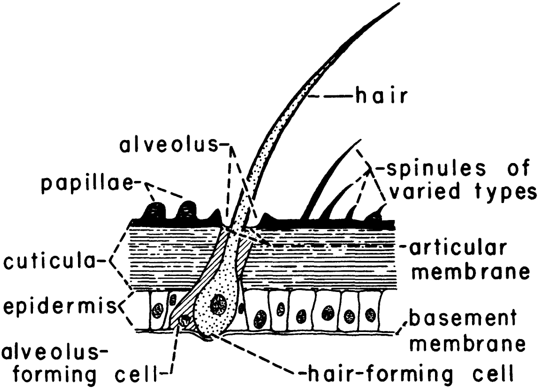

Fig. 9. External processes of body wall, diagrammatic. (Adapted from Comstock, 1920 and Snodgrass, 1935.)

can be either larger or smaller than the atrial opening. The wall of the atrium is frequently the most heavily sclerotized portion of the spiracle. The atrial opening may be on the same level as the remainder of the integument, or slightly raised or on a distinct papilla, with all degrees in between. In most of the tuberculate ponerine larvae the spiracles are mounted on papillae.

As a general rule all species of a genus have the same type (or types), but this is no assurance that this will hold true when more species are studied, for we have found several cases where the first and second types were found in different species of the same genus, in different colonies of the same species, in different larvae of the same colony and even in different somites of the same larva.

CUTICULAR PROCESSES OF THE BODY

We recognize, as a matter of convenience, three kinds of cuticular processes of the body: (1) spinules, (2) sensilla and (3) hairs (Fig. 9).

1. SPINULES—These are the "small spines" and the "minute points or nodules (scobinations)" under Snodgrass' (1935) rubric, "Non-cellular Processes of the Body Wall." See Fig. 10.

Most ant larvae have spinules only, but in *Eciton, Neivamyrmex, Labidus, Simopelta* (immature) and *Platythyrea* some or most of the spinules may be replaced by minute papillae (= nodules = granules = scobinations).

The following discussion of spinules is concerned only with mature worker larvae.

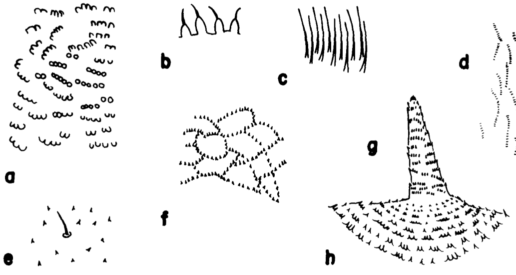

Fig. 10. External processes of body wall: a, papillae; b, spinules with conical base and sharp point; c, hairlike spinules; d, spinules arranged in transverse rows; e, isolated spinules; f, spinules in reticulate pattern; g, spinules on tubercle; h, spinules in concentric rows around base of tubercle.

SIZE—All spinules are minute in comparison with the size of the whole larva. Nevertheless there are relative differences. Some we called exceedingly minute (0.001 mm long) (e.g., *Rhytidoponera, Ectatomma, Megaponera, Trapeziopelta, Anochetus*); others we called large or long (*Diacamma australis* 0.025 mm, *Bothroponera sublaevis* 0.018 mm, *Ponera* 0.0125 mm, *Hypoponera* 0.03 mm).

SHAPE—Most spinules have no distinctive shape even at high magnification, but in *Bothroponera sublaevis* we have described them as having a conoidal base and sharp point; in *Hypoponera* they are hairlike.

OCCURRENCE—We have found spinules in all subfamilies except Leptanillinae. We have found none at all in about 20% of the genera.

DISTRIBUTION—Spinules are generally distributed over the body surface in about a third of the genera. In 14% spinules are somewhat restricted. In another third they are so severely restricted that they are difficult to find.

ARRANGEMENT—By far the most common (65% of the genera) pattern of arrangement of the spinules is in transverse rows; in 12% they are isolated and show no pattern; in only 5% did we find a reticulate pattern. The majority (19 out of 27) of tubercle-bearing ponerine genera have spinules on the tubercles; in two species (*Mesoponera fauveli* and *Hypoponera iheringi*) spinules on the body are arranged in concentric circles around the bases of the tubercles.

TAXONOMY—The taxonomic usefulness of body spinules is limited at the generic level and we have rarely had occasion to use them. Future studies may show them to be more useful at the species level.

2. SENSILLA. A sensillum[1] is a thin disc, from the center of which

[1] "Sensillum (pl. *sensilla*).—A coined word (from L. *sentio*, perceive) meaning a sense organ. Sometimes used in the feminine (*sensilla, ae*), but it is presumptuous to give sex gender to words not in the language of their origin." (Snodgrass 1960: 270.)

arises a minute hairlike structure less than 0.009 mm long. Sensilla are few and widely scattered over the body integument. As it is difficult to distinguish a sensillum from a minute hair with alveolus and articular membrane, we have made an arbitrary division at 0.003-0.009 mm. If the hair is shorter than 0.003 mm, we call the structure a sensillum; if it is longer than 0.009 mm, we call it a hair; between these limits we call it a sensillum if there are no hairs on the body and a hair if there is on the larva a transition to larger hairs. But our limits are artificial: any hair shorter than 0.009 mm undoubtedly serves a sensory function regardless of what it is called. "The sense organs in which the external part has the form of a seta, or is clearly derived from a hairlike process of the cuticula, retain essentially the structure of a seta [= hair] with its associated cells in the body wall, to which is added a sense cell having its distal process connected with the base of the seta or extending into the hollow of the latter" (Snodgrass 1935: 515).

3. HAIRS. We have deliberately used this term for any slender elongate projection from the body wall, which is longer than 0.003 mm. Most of these projections are setae as defined by Snodgrass (1935): a seta is "a hairlike unicellular external process of the body wall or of any derivative of the latter." "Each seta . . . arises from a cup-like cavity in the cuticula, the *alveolus*, situated at the outer end of a perforation of the cuticula, the *trichopore*; and each seta is united at its base with the wall of the trichopore by a ring of thin membrane, the *articular membrane* of the seta" (Comstock 1925: 32). However, we have often found processes similar in size and shape to "setae" and intermingled among "setae", but lacking the alveolus and articular membrane. Hence we have adopted the noncommital but descriptive term "hair."

BODY HAIRS

The hypothetical typical ant larva would be abundantly clothed with smooth, unbranched, slightly curved hairs which would range in length from 0.05 to 0.2 mm and which would be uniformly distributed. *Stigmatomma* is a very close approximation.

LENGTH—The hairs of ant larvae range in length from 0.003 mm to 0.6 mm. Extremes are not numerous on any larva. At the lower end (see above under "Sensilla") hairs measuring 0.003-0.008 mm are to be found in 16 genera, only *Vollenhovia* having the minimum. At the upper end we have found three genera with hairs measuring 0.5 mm (*Camponotus, Meranoplus* and *Ectatomma*) while hairs of *Myrmecia* and *Pristomyrmex* reach 0.54 mm and those of *Allomerus* (sexual) 0.6 mm.

ABUNDANCE—Referring to the number of body hairs on a larva we have used the terms "dense," "abundant," "numerous," "sparse" and "few," but we find them vague and unsatisfactory. Since they are qualitative terms, there is overlapping. Furthermore, appearance can deceive: a larva with branched hairs can appear to be densely clothed while the same number of unbranched hairs would appear sparse; also short hairs would appear sparser than the same number of long hairs.

It would be an arduous task to count the hairs on every larva studied, but one might count a representative unit-area and multiply by the estimated surface area of the body. Recently we did this for a few species; the results were: *Camponotus* (*Myrmentoma*) *nearcticus* 14,276 (=

dense); *Pogonomyrmex salinus* 2563 (= numerous); *Amblyopone australis* 1642 (= numerous); *Azteca alfari* 296 (= sparse); *Clarkistruma alinodis* 200 (= sparse); *Tapinoma luteum* 60 (= sparse).

We have applied the term "dense" to about 8% of the genera, "numerous" to 42%, "sparse" to 38% and nearly naked to 10% (7 genera in Attini, 10 in Dolichoderinae). In eight genera (all in the Ponerinae) we have found naked larvae, i.e., no hairs on body or tubercles: *Bothroponera denticulata, Discothyrea, Megaponera, Mesoponera melanaria, M. wroughtoni, Ophthalmopone, Proceratium, Psalidomyrmex, Thaumatomyrmex.*

DISTRIBUTION—In most genera body hairs are uniformly distributed. In many, however, there are concentrations or deficiencies or absences in certain areas.

CLASSIFICATION OF HAIR-TYPES—When the larvae of only 20 genera were known, W. M. Wheeler stated (1910: 73) that the hairs show a "bewildering diversity of form." What would he say about the variety described and figured below (Fig. 11)?

The following scheme for classifying the 29 hair-shapes which we have found among ant larvae is a matter of convenience; some other scheme would doubtless be just as good. Furthermore ours is artificial. Frequently there is a graded transition between the extremes; we have called the extremes two types and ignored the intergrades. For example, when a larva has unbranched, bifid and multifid hairs, we have made three types, because other species may have only unbranched or only bifid or only multifid. In parentheses we have given the range in length of the type.

I. UNBRANCHED.

A. SMOOTH. There are no denticles; the shaft is smooth and tapers evenly and gradually to a sharp point. We have usually called such hairs "simple."

1. SLIGHTLY CURVED OR STRAIGHT. (0.003-0.53 mm) If straight with rather stout base and sharp point, this might be called spikelike. Occurence: 83 genera. Dominant in 27 genera.

2. FLEXUOUS. (0.03-0.5 mm) Occurrence: 42 genera. Dominant in 8 genera. In descriptions we have called this type "flexible," "flexuous," "sinuous," "lashlike," "whiplike" or "flagelliform."

3. UNCINATE. (0.035-0.32 mm) The tip of the hair is curved into a single sharp-pointed hook, which may be larger or smaller than or equal to the shaft in diameter; the shaft may be straight, sinuous, sigmoid or spiral. This type is not common and there are only a few on any larva. Occurrence: CERAPACHYINAE—*Lioponera;* MYRMECIINAE—*Myrmecia;* PONERINAE—*Rhytidoponera* (young only); PSEUDOMYRMECINAE; MYRMICINAE—*Cataulacus, Hylomyrma* (sexual), *Solenopsis* (1 species), *Stenamma;* DOLICHODERINAE—*Azteca;* FORMICINAE—*Calomyrmex, Camponotus, Echinopla, Polyrhachis.*

4. ANCHOR-TIPPED. (0.05-0.45 mm) The shaft is stout and straight or sinuous or sigmoid or spiral; the tip is stout and with two sharp-pointed hooks like an anchor. Usually in transverse rows across the dorsum, one row per somite and not more than nine per row. Occurrence: MYRMICINAE—28 genera.

B. DENTICULATE. Minute side branches, called denticles, off the main shaft.

1. DENTICULATE THROUGH MOST OF LENGTH. (0.01-0.6 mm) Occurrence: 29 genera. Dominant in 10 genera.

2. FLEXUOUS AND DENTICULATE. (0.09-0.16 mm) Occurrence: *Aspididris, Basiceros, Rhopalothrix* (immature), *Strumigenys;* dominant in first 3 genera.

3. DENTICULATE ON DISTAL HALF ONLY. (0.002-0.42 mm) Occurrence: 16 genera. Dominant in *Cardiocondyla, Melophorus, Pogonomyrmex.*

4. TIP DENTICULATE (we have also called this "tip frayed"). (0.009-0.25 mm) Occurrence: 20 genera. Dominant in *Lophomyrmex, Ocymyrmex.*

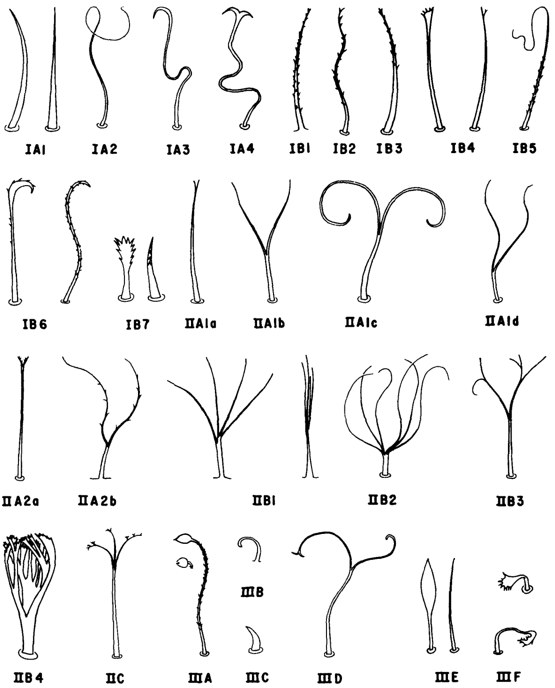

Fig. 11. Hair classification. For explanation see text.

5. FLAGELLIFORM WITH BASE DENTICULATE. (0.3-0.5 mm) Present and dominant in one genus (*Ectatomma*).

6. UNCINATE AND DENTICULATE. (0.032-0.54 mm) The tip of the hair is curved into a single sharp-pointed hook; the shaft may be straight or sinuous. Occurrence: *Crematogaster, Hylomyrma* (sexual), *Myrmecia harderi* and young of 5 species, *Myrmica, Rhopalothrix* (immature), *Tetraponera allaborans.*

7. FLATTENED DISTALLY, MARGINS DENTICULATE. (0.013-0.09 mm) Occurrence: *Eubothroponera, Heteroponera, Lasius* (*Chthonolasius*), *Stigmacros.*

II. BRANCHED. The hair arises singly from the integument but divides at approximately the same point into two or more shafts.

A. ~~SMOOTH~~. BIFID

1. ~~BIFID~~. SMOOTH

a. TIP BIFID. (0.02-0.31 mm) Occurrence: 18 genera. Dominant in *Cataulacus, Cryptocerus, Formica, Phyracaces, Stenamma, Trigonogaster.*

b. DEEPLY BIFID. (0.024-0.3 mm) Occurrence: 11 genera. Dominant in *Acanthognathus, Eusphinctus, Ischnomyrmex, Rhytidoponera.*

c. DEEPLY BIFID, TIPS CURLING IN OPPOSITE DIRECTIONS. (0.018-0.15 mm) Occurrence: 13 genera. Dominant in *Carebara, Colobostruma, Mayriella, Oligomyrmex, Paedalgus, Pheidologeton.*

d. DEEPLY BIFID, BRANCHES LONG AND FLEXUOUS. (0.027-0.28 mm) Occurrence: 16 genera. Dominant in *Apsychomyrmex* and *Chelaner.*

2. PARTLY DENTICULATE.

a. TIP BIFID AND DENTICULATE. (0.009-0.25 mm) Occurrence: 8 genera. Dominant in *Cataulacus* and *Tetramorium.*

b. DEEPLY BIFID, BRANCHES DENTICULATE. (0.014-0.25 mm) Occurrence: 11 genera. Dominant in *Daceton, Epopostruma, Mesostruma, Orectognathus, Phyracaces, Pristomyrmex, Smithistruma, Strumigenys.*

B. MULTIFID AND SMOOTH. In some genera the branches are in the same plane; in descriptions we have called these "palmate" or "palmately branching."

1. BRANCHES SHORT. (0.009-0.35 mm) Occurrence: 17 genera. Dominant in 11 genera.

2. BRANCHES LONG AND FLEXUOUS. (0.032-0.35 mm) Occurrence: 12 genera. Dominant in 7 genera.

3. BRANCHING DICHOTOMOUSLY. (0.01-0.12 mm) Occurrence: 2 genera (*Aphaenogaster* and *Dolichoderus*).

4. BRANCHING DENDRITICALLY. (0.036-0.22 mm) Occurring and dominant in *Anergates* and *Anergatides.*

C. MULTIFID, BRANCHES DENTICULATE. (0.025-0.14 mm) Occurring and dominant in *Calyptomyrmex* and *Rogeria.*

III. MISCELLANEOUS

A. CAPITATE. (0.018-0.17 mm) Occurrence: 3 genera (*Bothroponera, Eurhopalothrix, Rhopalothrix.*)

B. VERY SHORT, TIP HOOKED AND SHARP-POINTED. (0.009-0.027 mm) Occurrence: 3 genera (*Acromyrmex, Crematogaster, Solenopsis.*)

C. CLAWLIKE. (0.027 mm) Occurrence: 1 genus (*Acromyrmex*).

D. BIFID, HOOKED AT TIPS. (0.054-0.13 mm) Occurrence: 1 genus (*Chelaner*).

E. LANCEOLATE. (0.027-0.09 mm) Occurrence: 1 genus (*Messor*).

F. ANGULATE NEAR MIDDLE, DENTICULATE AT TIP. (0.009-0.072 mm) Occurrence: 2 genera (*Allomerus* and *Crematogaster*).

The number of body-hair types per genus for the subfamilies is shown in Table 1. It is obvious from the table that the Myrmicinae and Formicinae show the greatest variety, which is not surprising, since they are the largest subfamilies.

TABLE 1. Number of body-hair types per genus

Number per genus	1	2	3	4	5	6	7
Dorylinae	3	3					
Leptanillinae		1	1				
Cerapachyinae	1	2	1				
Myrmeciinae					1		
Ponerinae	26	4	2		2		
Pseudomyrmecinae			4				
Myrmicinae	21	31	22	3	1	2	1
Aneuretinae			1				
Dolichoderinae	8	4	1				
Formicinae	5	7	9	2	1	1	1
TOTALS	64	52	41	5	5	3	2

The genera with the greatest variety are: *Crematogaster*, 6 (but a species has only 2 or 3 types); *Pristomyrmex*, 6 (species with 4-6 types each); *Polyrhachis*, 6 (3-5 per species); *Solenopsis*, 7 (2 or 3 per species); *Camponotus*, 7 (2-5 per species).

TAXONOMY—In classifying at the generic level we have not used hair characters as much as we might, because we have not needed to. Their utility is somewhat impaired by interspecific differences and intraspecific variability. If ant larvae are ever studied at the specific level, hair characters will undoubtedly be employed.

FUNCTIONS OF HAIRS—The body hairs of ant larvae may serve one or more of the following functions:

1. Support. Larvae usually lie on the side or back. Hairs would lift them above a damp substrate and allow a little ventilation.
2. Regulation of Temperature. The nearly dead air space among the hairs insulates against rapid change of temperature.
3. Regulation of Humidity. The nearly dead air space tends to prevent dessication.
4. Defense. Hairs may afford some protection against cannibalism.
5. Clumping. The first mention of a function of anchor-tipped hairs is given by Janet (1892: xcvii-xcviii): "On sait que les Fourmis saisissent délicatement entre leur mandibules et transportent très fréquemment leur progéniture d'un point à un autre de leur nid pour la mettre constamment dans les meilleures conditions possibles . . . . Pour que ces transports ne prennent pas un temps par trop considérable, les oeufs et les très jeunes larves sont transportés par paquets, souvent assez volumineux. . . . Pour les larves, l'agglutination se fait par l'accrochage d'un certain nombre de poils disposés régulièrement sur chaque segment, très longs, terminés par des crochets ou des ancres et offrant une disposition mécanique remarquable. Pour éviter les accidents qui pourraient résulter de la traction de ces poils d'accrochage sur la délicate cuticle chitineuse qui les porte, ils présentent tous, dans leur partie moyenne, une forte et brusque ondulation en forme d'un C ou en forme d'un S; le poil jouit, par suite de cette forme, d'une grande élasticité. Ces poils sont ainsi de véritables *poils d'accrochage à ressort*." Janet (1904: 33) stated that the young larvae of *Lasius*, which lack anchor-tipped hairs, were held together in packets by their long flexuous hairs. We have seen larvae of many other species clumped together; we have mentioned and figured this clumping in *Rhytidoponera* (1964c: 449) and *Camponotus* (1968: 216).
6. Suspension. Janet (1904: 33) made note of another function of hairs: "Les poils à double crochet des jeunes larves de Tetramorium caespitum sont pourvus de nombreuses sinuosités qui leur donnent beaucoup d'élasticité. Dans les nids artificiels de cette espèce, j'ai vu fréquemment un grand nombre de petites larves accrochées sur les parois verticales des chambres d'habitation. . . . Les ancres de ces poils pénètrent dans les aspérités de la paroi du nid."

Donisthorpe (1927: 197) observed in 1911 that many of the larvae of *Tetramorium caespitum* were hung on the plaster walls of his observation nest by their anchor-tipped hairs.

Eidmann (1928: 239) thought it likely that *Camponotus* larvae might be hung on the vertical walls of the nests in tree trunks, but regarded it

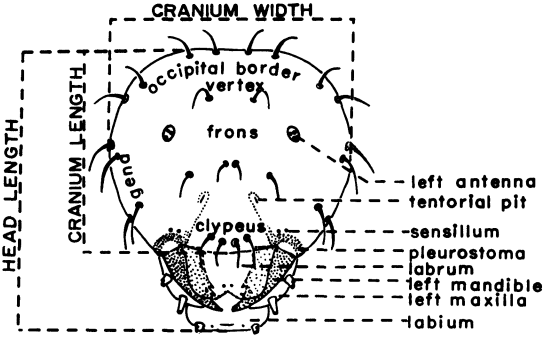

Fig. 12. Hypothetical generalized head in anterior view.

as impossible for one to open a trunk fast enough to find the larvae undisturbed by alarmed workers.

We have often collected live samples from *Crematogaster* colonies into large plastic vials; we always put a label on heavy paper in each vial. Invariably by the time we get back to the laboratory the larvae are hung on the label by their anchor-tipped hairs. Whenever we see this, we think of a papoose suspended from a tree trunk out of harm's way.

When a worker seizes a single larva from a packet or hanging on a wall, and carries it away, why isn't the hair jerked loose from the cuticle? Presumably the curves or twists in the shaft of the hair, when straightened out by pulling, impart a rotation to the hook which tends to disengage it.

7. Reception of Stimuli. "Finally, there is associated with many insect setae, if not the majority of them, a sensory nerve cell, lying in or just beneath the epidermis, that is connected with the seta by a distal nerve process. Setae thus innervated become setal sense organs." (Snodgrass 1935: 57-58.)

8. Holding Food. In the Attini, Weber (1972: 39-42) reported that all the larvae use the ventral thoracic hairs mainly for keeping the fungus within reach of the mouth parts.

HEAD

ORIENTATION—We follow Snodgrass (1935) in regarding the head of an ant—either larva or adult—as being hypognathous.[2] Consequently in all our papers on ant larvae (except Dorylinae 1943) we have considered the face to be anterior and the vertex dorsal, while the mouth parts are directed ventrally (see Fig. 12-14).

[2] The terms *orthocephalic* and *hypocephalic* were coined by Emery in 1899 (p. 6): —" . . . i primi segmenti postcefalici sono più sviluppati nella parte dorsale, accorciati nella parte ventrale, per cui, sul profilo, appariscono come disposti a ventaglio, il loro contorno dorsale formando complessivamente una curva o gobba che costituisce l'estre-

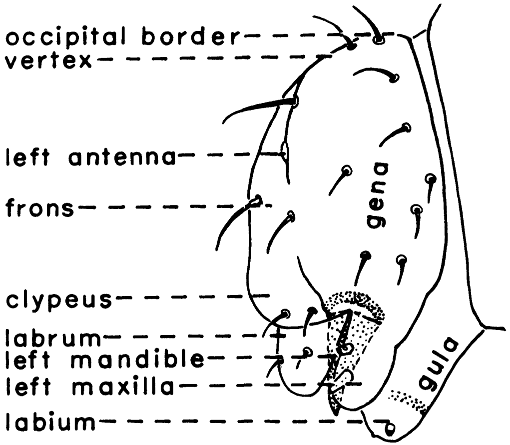

Fig. 13. Hypothetical generalized head in side view.

SIZE—The heads of ant larvae are rather small, but not minute. In the mature worker larvae the length ranges between 0.06 and 0.14 of body length. In certain species of sawflies the ratio is 0.1 and 0.13; in two species of caterpillars it is 0.11 and 0.12; in a white grub (Coleoptera) it is about 0.15. In other words, the relative sizes of the heads of mature ant larvae overlap those of the larvae in other insect orders.

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mità anteriore apparente della larva, mentre il capo, ossia l'estremità anteriore morfologica trovasi collocato sulla faccia ventrale del corpo. Perciò queste larve possono dirsi *ipocefale,* a differenza di quelle del maggior numero delle altre formiche, che diremo *ortocefale.*"

[" . . . the first postcephalic segments are better developed dorsally, shortened ventrally, so that, in profile, they resemble a ventail, their dorsal contour forming on the whole a curve or hump which constitutes the apparent anterior extremity of the larva, while the head, which is the morphological anterior extremity, is located on the ventral surface. For this reason these larvae may be called *hypocephalic,* in contradistinction to those of the greater number of other ants, which we shall call *orthocephalic.*" (1972b.)]

We have abandoned the use of these terms because (1) they are used in Egyptology and physical anthropology with quite different meanings. (2) The terms are incorrectly derived: *hypocephalic* should mean "under the head" (cf. *hypodermic*) and *orthocephalic* "straight-headed"; but in certain ant larvae the head is "under" the body and in others it is the body that is straight; hence *hyposomatic* and *orthosomatic* would have been more appropriate. (3) The larvae of many species are intermediate in varying degrees between the extremes.

We used Emery's terms in earlier papers, but recently we have preferred to repeat descriptions rather than to coin new terms, which are really not very useful.

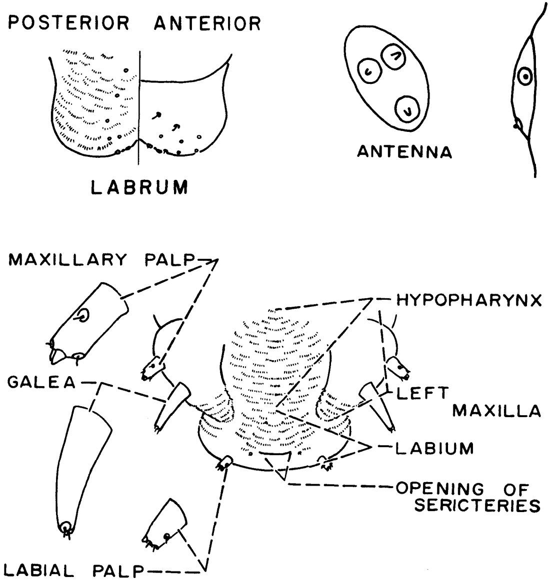


Fig. 14. Parts of hypothetical generalized head, enlarged.

In our descriptions of ant larvae we have used vague terms, such as "large" or "small;" recently we have used small if the ratio of head length to body length was about 0.06 and large if it was 0.14. In between we have not considered it worth mentioning and we now doubt if head size need be mentioned at all. For one reason, one must be sure he has a mature larva, since the head is relatively very large upon hatching, but becomes relatively smaller as the larva grows. For example, the ratios in *Aphaenogaster rudis* are 1st instar 0.29, 2nd instar 0.29, 3rd instar 0.27, 4th instar 0.23, mature larva 0.1.

SHAPE—In our descriptions of ant larvae we have rarely considered the shape of the head as a whole, i.e., cranium plus mouth parts, but we have in nearly all cases described the shape of the cranium in anterior view. This shape is difficult to describe except at length and in detail, using an amount of space which it does not merit. The easiest method we have found to be comparison with a geometric figure, which requires one

word. Since sharp angles are rare in ant larvae, we have prefixed the geometric term with the Latin *sub-*, "somewhat," to avoid specious precision. The advantage of this procedure is that the describer is limited only by his knowledge of plane geometry and his imagination in transposing curves into angles. But imagination also has a disadvantage: the same cranium shape may be transposed into more than one geometric figure. For example, in *Notoncus* we have called the shape subhexagonal at one time and transversely subelliptical at another. We would be willing to call the *Formica* cranium shape transversely subelliptical or suboctagonal or subquadrangular or subcircular or subheptagonal.

Is cranium shape worth all this fuss? We doubt it. It might be used occasionally in generic differentiation, but so far it has rarely been needed. Furthermore, within some genera there are differences between species. For example, in *Dolichoderus* there are four cranial shapes; in *Crematogaster* there are six.

In spite of the above strictures we offer in Fig. 15 a classification of cranial shapes. In our hypothetical typical ant larva the cranium shape (in anterior view, see Fig. 12) is subhexagonal.

The cranium in side view rarely presents anything unusual; it is generally as in Fig. 13. The following exceptions deserve special mention because of the bulging on some part of the anterior or posterior surface: DORYLINAE—*Dorylus* (*Anomma*). PONERINAE—*Typhlomyrmex*. MYRMICINAE—*Apterostigma, Aspididris, Cataulacus, Cryptocerus, Rhopalomastix, Rhopalothrix*. DOLICHODERINAE—*Engramma.*

In addition to differences in the shape of the cranium there are differences in proportion. In 75% of the genera the cranium is wider than long; in 20% the maximum width is approximately equal to the length; in only 5% does the length exceed the width. In this last case the ratio is usually about 1.1 but in the Leptanillinae (*Leptanilla* 1.47-1.6, *Leptomesites* 1.58) and in certain genera in the myrmicine tribe Myrmecinini (*Pristomyrmex* 1.54-1.71, *Myrmecina* 1.85, *Apsychomyrmex* 1.36) the excess is so great as to impart a grotesque appearance.

CLYPEUS—The junction of labrum to clypeus is usually indicated by a transverse groove on the anterior surface. The sides of the clypeus are marked by short grooves extending upward from each end of this transverse groove. The clypeus is further evidenced by a transverse row of 4-6 hairs, which are usually isolated from the other head hairs.

GULA—We go back to W. M. Wheeler's (1910: 18) description of the adult head: "the ventral portion [he evidently considered the head to be prognathous] of the head, bounded in front by the labium, on the sides by the cheeks and extending to the occipital foramen, is the throat, or gula. It is well-developed in the ants and is usually divided in two equal halves by a longitudinal suture." And finally we go back to the Latin, where *gula* = throat. Justified or not we have used "gula" for the posterior surface of the head and consequently we are stuck with it. But we haven't used it very often, for there is little to be said about it—much less, in fact, than we have said about the word. Evidently it is so effectively shielded by the body that there has been little evolutionary necessity or even opportunity for structures to develop on its surface.

CUTICULAR PROCESSES—A small portion of the cranial surface is spinulose in 14% of the genera. The spinules are restricted to the gula

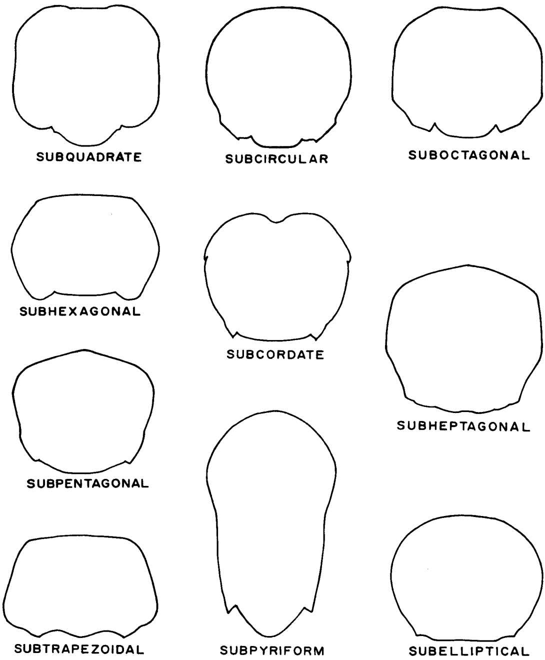


Fig. 15. Classification of head shapes.

in nine of these genera. The spinules are replaced by papillae in *Diacamma* and partly replaced by papillae in *Bothroponera*. *Diacamma* is the only genus in which we have found the entire cranium covered with spinules or papillae. In *Myrmecia* the clypeus is granulose. The cranium also bears sensilla, usually few, but numerous in *Myrmecia* and *Paraponera*.

SCLEROTIZED STRUCTURES—The anterior tentorial pit is usually surrounded by a ring which is more heavily sclerotized than the remainder of the head capsule. From the pit a bar frequently extends down to the anterior condyle of the mandible and continues as the pleurostoma to the posterior condyle; these may be as heavily sclerotized as the mandible but

are usually less so. In the myrmicine tribe Crematogastrini there is a sclerotized cross-bar inside the head just above the mouth parts; from each end of this a sclerotized structure extends onto the prothorax at the sides of the head. In the myrmicine tribe Attini in the genera *Myrmicocrypta, Apterostigma* and *Trachymyrmex* a similar dark staining structure is present on the prothorax at the sides of the head.

ANTENNAE

Adlerz was probably the first to suspect the true nature of the antennae: "Eyes are lacking, but some small pointed outgrowths of the anterior surface of the head are probably to be regarded as antennae" (1886: 50, translated from the Swedish). Emery (1899: 7) was the first to make positive indentification: "un paio di piccole appendici del capo che considero come rudimenti di antenne." That they were not discovered earlier is not surprising: (1) they are not pigmented; (2) ant larvae had been ignored.

SHAPE—Among ant larvae the typical antenna is a distinct low circular convexity with three sensilla (see Fig. 16), each of which bears a minute spinule.

Usually the antenna is only slightly elevated from the general cranial surface, but in 15% of the genera it is mounted on a low base.

Two genera have the antennae in depressions: *Calyptomyrmex* in shallow concavities; *Ocymyrmex* in pits.

In *Tetraponera natalensis* each antenna is represented by 3 individually raised sensilla on a small base (1973c).

Antennae of unusual shapes are to be found among the Ponerinae. In *Platythyrea* each antenna is a slender elongate lobose adnate elevation, narrowed dorsally to a slender ridge, which extends obliquely almost to the center of the occipital border; the sensilla are on and near its lower end. The antennae are small paraboloidal knobs in *Rhytidoponera, Heteroponera, Ophthalmopone* and *Neoponera*. In *Typhlomyrmex, Gnamptogenys* and *Ectatomma* the antennae are subcylindrical, project conspicuously and really look one-segmented.

POSITION—The antennae of ant larvae are mostly on the upper half of the cranium. We have based our measurements on our published drawings of the head in front (= full face) view. In this view the top of the drawing is the highest point on the occipital border; the bottom is the lowest point on the labium. The length of the cranium is measured from the highest point on the occipital border to the lowest point on the clypeus. In determining the position of the antennae we have measured from the highest point on the occipital border down the midline of the cranium to the level of the center of the antennae.

The antennae of 48% of the genera are above the middle; those of 40% are at the middle; of the 12% below the middle, 8% are above the lower third and 5% are at the lower third. Therefore it can be stated that the antennae of ant larvae are at or above the lower third of the cranium and most (88%) are at or above the middle.

Later in this memoir we use the position of the antennae as a character to separate ant larvae from the larvae of other aculeate Hymenoptera. Employing the same technique we find that antennae of the

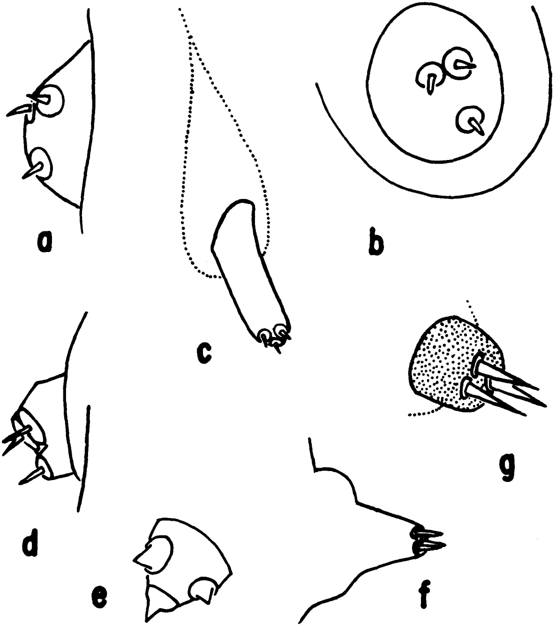


Fig. 16. Antennae. a and b, side and anterior views of typical antenna (*Pogonomyrmex barbatus*); c-f, specialized antennae: c, *Gnamptogenys* sp., in anterior view; d, *Alistruma* sp., in side view; e, *Tetraponera aitkeni* (first instar), in side view; f, *Rhytidoponera impressa*, in anterior view; g, *Gnamptogenys striatula*, in anterior view. (All of left antenna.)

latter are all at or below the middle of the cranium, while most of those measured (83%) are at or below the lower third.

In two ant genera—*Phyracaces* and *Myopias*—the antennae are so high (at the uppermost fifth) that they impart a grotesque appearance to the face.

Usually the two antennae are well separated, as would be expected by anyone accustomed to looking insect larvae in the face: the distance between them is somewhere near one-half the greastest width of the cranium,

but ranging between one-third and two-thirds. In two ant genera they are so close together as to appear grotesque: *Myopias* (one-ninth the width) and *Myrmecina* (one-fifth the width).

SIZE—We have been altogether too casual about the size of the antennae: we have called them minute, small, medium, or large merely by inspection of the finished drawing. We have not considered it worthwhile getting precise measurements and ratios. Nevertheless to check on our impressions, we have recently divided the maximum width of the head on the drawing by the width of the antenna. If the quotient is 19 or less we call the antenna large; if it is between 19 and 27 we call it medium; above 27, small. On this scale 39% of the genera have large antennae, 46% medium and 28% small.

SENSILLA—The antennae of the vast majority (73% of the genera) of the ant larvae studied have three small sensilla. In 10% there are two sensilla, while 18% have a variable number. In 9% there are either two or three sensilla; in 5% three or four; in one genus (*Onychomyrmex*) two to four; in one (*Daceton*) three to five; in one (*Crematogaster*) one to four. The maximum number of sensilla on one antenna is five and the minimum one; no antenna is without sensilla.

Each sensillum bears a single spinule, which is almost invariably minute, but in the ponerine genera *Typhlomyrmex, Gnamptogenys* and *Ectatomma* the spinules are long and stout.

HEAD HAIRS

ABUNDANCE—The overwhelming majority of ant larvae—60% of the genera—have few (i.e., less than 40) hairs on the head. In 20% the head hairs are moderately numerous (40-100). Only 10% have head hairs in abundance (100 or more), while 10% have no hairs at all on the head.

SIZE—For the family as a whole the head hairs range in length from 0.003 to 0.32 mm, which is less than the range for body hairs. The shortest are to be found in *Crematogaster*, the longest in *Gigantiops*.

SHAPE—We use the same scheme for classifying the shapes of the head hairs that we use for body hairs (see Fig. 11), but there are fewer types for the family: 29 shapes of body hairs but only 17 of head hairs. Our scheme follows; the size range of each type is given in parentheses.

I. UNBRANCHED

A. SMOOTH

1. SLIGHTLY CURVED OR STRAIGHT. (0.003-0.21 mm). This is the predominant type of head hair; it is to be found in 98 genera.

2. FLEXUOUS. (0.027-0.18 mm) Occurrence: 6 genera

B. DENTICULATE.

1. DENTICULATE THROUGH MOST OF LENGTH. (0.025-0.18 mm) Occurence: 16 genera.

2. FLEXUOUS AND DENTICULATE. (0.054-0.32 mm) Occurence: 8 genera.

3. DENTICULATE ON DISTAL HALF ONLY. (0.02-0.14 mm) Occurrence: 6 genera.

4. TIP DENTICULATE. (0.003-0.175 mm) Occurrence: 27 genera.

7. FLATTENED DISTALLY, MARGINS DENTICULATE. (0.003-0.08 mm) Occurrence: 2 genera (*Eubothroponera* and *Tetramorium*).

II. BRANCHED.
A. BIFID.
1. SMOOTH.
a. TIP BIFID. (0.009-0.126 mm) Occurrence: 22 genera.
b. DEEPLY-BIFID. (0.018-0.13 mm) Occurrence: 17 genera.
c. DEEPLY BIFID, TIPS CURLING IN OPPOSITE DIRECTIONS. (0.027 mm) Occurs in only one genus (*Paedalgus*).
2. PARTLY DENTICULATE.
a. TIP BIFID AND DENTICULATE. (0.035-0.05 mm) Occurrence: 3 genera (*Pheidole, Rogeria, Myrmecorhynchus*).
b. HALF-BIFID, BRANCHES DENTICULATE. (0.054-0.09 mm) Occurrence: 4 genera (*Gnamptogenys, Oligomyrmex, Rogeria, Camponotus*).
B. MULTIFID AND SMOOTH.
1. BRANCHES SHORT. (0.045-0.21 mm) Occurrence: 11 genera.
3. BRANCHING DICHOTOMOUSLY. (0.025-0.05 mm) Occurs in only one genus (*Aphaenogaster*).
C. MULTIFID, WITH BRANCHES DENTICULATE. (0.025-0.088 mm) Occurrence: 1 genus (*Calyptomyrmex*).
III. MISCELLANEOUS.
B. DENTICULATE, TIP CLUBBED OR SPATULATE. (0.05 mm) Occurs in only one genus (*Acromyrmex*).
C. VERY SHORT, TIP HOOKED AND SHARP-POINTED. (0.006-0.02 mm) Occurs in only two genera (*Crematogaster* and *Solenopsis*).
G. ANGULATE AT MIDDLE, DENTICULATE AT TIP. (0.012-0.018 mm) Occurs in only one genus (*Allomerus*).

DISTRIBUTION—The exact number and precise location of hairs does not seem to be of much importance among ant larvae: consequently we have rarely mentioned them. Head hairs are usually approximately bilaterally symmetrical. In most genera (74%) there are no hairs between the antennae, but in 26% there are. One instance of taxonomic significance is to be found in the formicine tribe Camponotini: there is a conspicuous naked area in the form of an inverted V, with the apex on the vertex and the arms extending downward on the frons.

NUMBER OF HAIR-SHAPES PER GENUS—Not only are there fewer shapes among head hairs than among body hairs, but there are fewer shapes per genus: one shape in 75% of the genera; two in 17%; three in 5%; four in three (*Echinopla, Polyrhachis* and *Camponotus*); and five in one (*Oligomyrmex*).

COMPARISON OF HEAD HAIRS WITH BODY HAIRS—*A priori* one might expect head and body hairs to be similar, but such is not the case. In only 21% of the genera are they alike in abundance, size and shape, but in 25% they differ in all three respects. In 10% they are alike in abundance and size but differ in shape; in 9% they are alike in abundance and shape but differ in size; in 4% they are alike in size and shape but differ in abundance. In 20% of the genera they are alike in abundance only; in 9%, in size only; and in 6%, in shape only. In other words head hairs are similar to body hairs in 20% of the genera, while they differ in 80%.

MOUTH PARTS

Ant larvae are equipped with a standard set of insect mouth parts (see Fig. 12 and 14): a labrum, a pair of mandibles, a pair of maxillae, a labium and a hypopharynx. These are never so specialized that any part is lacking or even greatly reduced in comparison with its fellow-parts.

These mouth parts differ from those of adult insects in that they are never heavily sclerotized throughout. Their only sclerotized parts are the mandibles, palps and galeae. Nevertheless the mouth parts of ant larvae are not to be thought flabby: they do maintain a definite form within narrow limits. The labrum, mandibles and maxillae are movable; so is the labium. The latter is also capable of change of shape.

The mouth parts are best developed in size and complexity in the Leptanillinae, Myrmeciinae, Ponerinae, Myrmecinini and Basicerotini. They are feebly developed—almost vestigial—in the Myrmicariini, Crematogastrini, Attini and Dolichoderinae. In all other taxa they may be considered intermediate.

The main function of the mouth parts is ingestion of food. The labrum, maxillae and labium may hold food until it can be ingested; they also have a sensory function. The mandibles may also aid in holding food.

Mandibles are capable of active motion from side to side; hence, if they are long enough, their teeth could work against each other. In three genera (*Bothriomyrmex, Technomyrmex* and *Apterostigma*) the mandibles are so short that they do not even meet; in 22 genera they are short but meet in the midline; in all other genera they are long enough to cross at the midline. Hence the more robust mandibles are thought to be able to comminute such food as insect fragments. Perhaps they can, but they simply do not look rugged enough to do any cutting, although they may be capable of a limited amount of crushing. It is certain that such food can be ingested, for we have often found chitinous fragments of insects in the meconium. But that does not prove the cutting power of the mandibles; it is conceivable that the soft portions of the food might be digested enough externally to dissociate the parts of the insect prey before ingestion.

It is more likely that the comminution is effected by the rubbing together of the various spinules and ridges on the several mouth parts. See Fig. 17.

The coarse sharp spines on the mandibles of attine larvae puncture egg shells, fungus hyphae and gongylidia.

A communicative function of the mouth parts was postulated by W. M. Wheeler (1920: 48): when there is no food between the spinulose surfaces of the mouth parts, they might stridulate and apprise the workers of the larva's hunger.

Another conceivable function might be locomotor. The mandibles in *Dinoponera, Trapeziopelta, Typhlomyrmex, Leptogenys* and *Daceton* have the apical portion of the mandibles curved posteriorly (instead of medially). These might serve as anchors for a lumbricoid locomotion, as do the mouth-hooks of maggots.

TROPHORHINIUM—The term "trophorhinium" was coined by W. M. Wheeler in 1920 (p. 48) and defined by him as a larval structure consisting of "two flat, opposable plates, the dorsal and ventral surfaces of the buccal cavity, each furnished with very fine, parallel, transverse striae or welts, which, under a high magnification are seen to be made up of minute chitinous projections or spinules." Referring to pseudomyrmecine larvae he added that "the two surfaces are evidently rubbed on one another and thus triturate the substance of the food pellet, only small portions of which are ingested at a time from the trophothylax." The

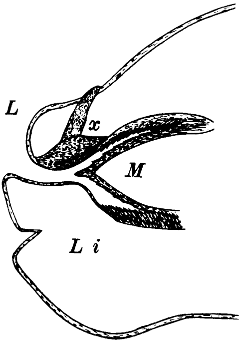


Fig. 17. Larva of *Camponotus americanus*. Longitudinal section showing arrangement of mouth parts: *L*, labrum; *Li*, labium; *M*, mandible; *x*, chilosclere. Note opposable spinules on posterior surface of labrum and anterior surface of mandible, and on posterior surface of mandible and anterior surface of hypopharynx.

trophorhinium may function also as a stridulatory organ, as mentioned above under "Mouth Parts."

G. C. Wheeler used the term in his early papers (1928, 1943, 1950), but we have not used it since, preferring to describe separately the spinules and ridges of each mouth part. It is not very useful since the trophorhinium does not actually exist as an organ; it is really a functional rather than an anatomical term.

LABRUM

The labrum is a thick flap attached to the ventral border of the clypeus (Fig. 18). Since it is a flexible organ, its form may vary, but we have recorded shape and proportions as we found them in preserved material.

We have made little use of the characters of the labrum in classification, because we have not needed them, but several may prove useful in future studies, such as size, shape and proportions; abundance, size and arrangement of spinules on the posterior surface; and the number and location of the sensilla.

SIZE—We have not always reported the size of the labrum. In only 6% of the genera have we called it large; in 47% we called it small; in 48% we have not mentioned size, which means that we considered the labrum medium.

SHAPE—The predominant shape (in anterior view) is bilobed due to a median impression of the ventral border; this we found in 56% of the genera; other shapes follow in numerical order: paraboloidal 13%, subrectangular 12%, subtrapezoidal 8%, trilobed 4%, lobose 2%, arcuate 2%; one genus each semicircular, subtriangular, crescentic and four-lobed.

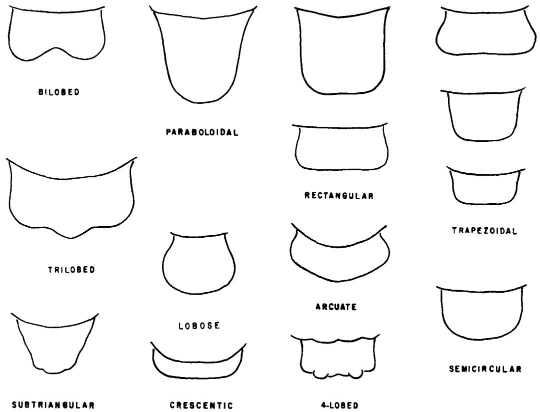


Fig. 18. Shapes of labrum in anterior view.

PROPORTIONS—In most genera (53%) the breadth is twice the length; in 9% it is three times the length; in 4 genera it is four times the length and in 1 it is six times. In 30% of the genera the breadth is somewhat greater than the length and in 5% they are equal. In only one genus (*Polyrhachis*) does the length exceed the breadth.

ANTERIOR SURFACE—The anterior, or exposed, side of the labrum bears hairs and/or sensilla and/or spinules. In 13% there are hairs (2-16); a few spinules are found in 8%; most genera have sensilla, but in 9% they are lacking; the maximum number of sensilla is 50 in *Bothroponera.* The sensilla are usually bilaterally symmetrical in arrangement.

VENTRAL BORDER—Many genera (41%) have a few sensilla on the ventral border, but a few (7%) have many. Spinules occur in a minority (27%).

POSTERIOR SURFACE—The posterior surface of the labrum of the larva is usually well endowed with sensilla and spinules (see Fig. 19). Sensilla are numerous (more than 10) in 35% of the genera, few in 57%, while 8% have none. Spinules are abundant in 55%, sparse in 11%, few in 20% and none in 14%. Wherever the spinules are arranged in a definite pattern we have mentioned it in our specific descriptions. Several of the common patterns are shown in Fig. 19, but we are not attempting here any summary. Sensilla and spinules are usually bilaterally symmetrical.

CHILOSCLERE—"We have coined this term from the Greek *cheilos,* lip, and *skleros,* hard, to designate the pair of conspicuous dark brown

17% and slender in 14%. The stoutest mandible is in *Iridomyrmex* (0.8) in the Dolichoderinae, and the most slender is in *Platythyrea* (3.4) in the Ponerinae.

It is obvious that mandible proportions are not very useful taxonomically. They can be used in characterizing some genera and a few larger taxa: in the Dolichoderinae and Formicinae they are stout; in the Ponerinae there is a tendency toward slenderness (4% stout, 58% intermediate, 38% slender.).

SCLEROTIZATION—The degree of sclerotization (= hardening) of the mandibles can usually be determined by the color. In unstained material feebly sclerotized mandibles are colorless like the integument of the head. With increasing sclerotization the color darkens from straw-colored through amber to dark brown. In material stained with acid fuchsin the corresponding change is from pale pink to deep red. Forty-eight per cent of the genera have moderately sclerotized mandibles, 28% heavily sclerotized, 24% have them feebly sclerotized. The hypothetical typical ant larva therefore has moderately sclerotized mandibles. The more specialized taxa generally have the mandibles feebly sclerotized, e.g., Dorylinae, Leptanillinae, Cerapachyinae, Proceratiini (Ponerinae), Crematogastrini (Myrmicinae), Attini (Myrmicinae), Dolichoderinae, Oecophyllini (Formicinae).

SHAPE—We have explained above our technique for classifying body shape. We have applied the same procedures to classifying and naming mandible shapes (in anterior view). The result was 18 types of mandible shapes (Fig. 20), which we now describe:

1. Ectatommoid—Subtriangular; with a medial blade arising from the anterior surface and bearing one or two medial teeth; apex curved medially to form a tooth. Occurrence: MYRMECIINAE: *Myrmecia*. PONERINAE: *Anochetus, Belonopelta, Bothroponera, Cryptopone, Ectatomma, Euponera, Gnamptogenys, Heteroponera, Hypoponera, Mesoponera, Mystrium, Neoponera, Odontomachus, Odontoponera, Pachycondyla, Paraponera, Ponera, Psalidomyrmex, Stigmatomma*. MYRMICINAE: *Acanthognathus, Calyptomyrmex, Chelaner, Clarkistruma, Colobostruma, Cryptocerus, Dacetinops, Dilobocondyla, Eurhopalothrix, Harpagoxenus, Huberia, Hylomyrma, Leptothorax, Liomyrmex, Macromischa, Manica, Mégalomyrmex, Meranoplus, Monomorium, Myrmica, Ocymyrmex, Orectognathus, Oxyepoecus, Paramyrmica, Procryptocerus, Rogeria, Solenopsis, Tetramorium, Vollenhovia, Xenomyrmex, Xiphomyrmex*.

2. Camponotoid—Subtriangular; base broad (width at least 2/3 the length); apex forming a round-pointed tooth; no medial teeth (or rarely one small one). Occurrence: MYRMICINAE: *Messor*. FORMICINAE: *Acanthomyops, Acropyga, Brachymyrmex, Calomyrmex, Camponotus, Dendromyrmex, Diodontolepis, Echinopla, Formica, Gesomyrmex, Gigantiops, Lasius, Melophorus, Myrmecocystus, Myrmecorhynchus, Notoncus, Opisthopsis, Paratrechina, Polyergus, Polyrhachis, Prenolepis, Prolasius, Stigmacros*.

3. Dolichoderoid—Basal part inflated and narrowed more or less abruptly to the distal part, which is slender and sharp-pointed; no medial teeth or blade. Occurrence: DORYLINAE: *Cheliomyrmex, Dorylus*. PONERINAE: *Discothyrea, Proceratium*. MYRMICINAE: *Apterostigma, Crematogaster, Myrmicocrypta*. DOLICHODERINAE: *Araucomyrmex, Azteca, Bothriomyrmex, Dolichoderus, Dorymyrmex, Engramma, Forelius, Froggattella, Iridomyrmex, Leptomyrmex, Liometopum, Tapinoma, Technomyrmex*. FORMICINAE: *Myrmelachista, Oecophylla*.

4. Pogonomyrmecoid—Subtriangular; with three conspicuous medial teeth, which are approximately in the same plane. Occurrence: PONERINAE: *Centromyrmex, Myopopone*. MYRMICINAE: *Aphaenogaster, Alistruma, Aspididris, Basiceros, Dacryon, Epopostruma, Machomyrma, Mesostruma, Novomessor, Podomyrma, Pogonomyrmex, Rhopalomastix, Rhopalothrix, Smithistruma, Stenamma, Strumigenys, Veromessor*.

5. Amblyoponoid—Narrowly subtriangular; without a blade; straight or with the apex slightly curved medially; with minute teeth on the medial border. Occurrence:

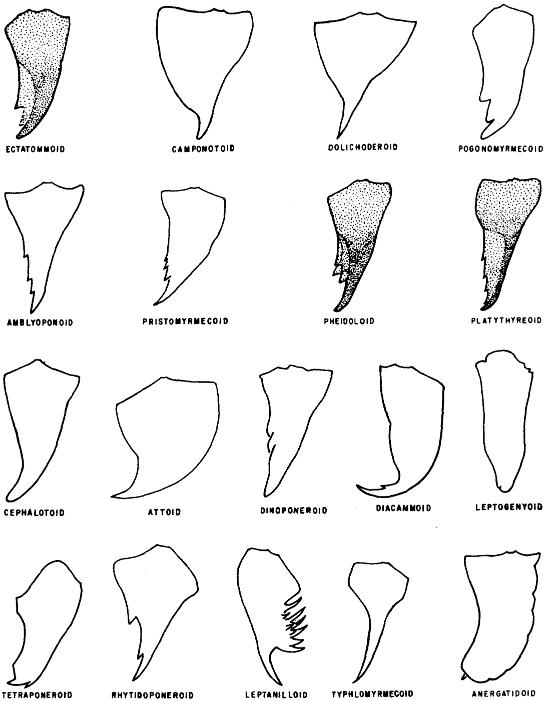


Fig. 20. Classification of mandible shapes. For explanation see text.

DORYLINAE: *Aenictus, Eciton, Labidus, Neivamyrmex.* CERAPACHYINAE: *Cerapachys, Eusphinctus, Lioponera, Phyracaces.* PONERINAE: *Amblyopone, Apomyrma, Onychomyrmex, Prionopelta.*

6. Pristomyrmecoid—Subtriangular; no medial blade; apical tooth curved medially and usually acute; subapical medial teeth small Occurrence: PONERINAE: *Hagensia.* PSEUDOMYRMECINAE: *Pachysima, Pseudomyrmex.* MYRMICINAE: *Apsychomyrmex, Cataulacus, Macromischoides, Meranoplus, Myrmecina, Myrmicaria, Pheidologeton, Pristomyrmex, Tranopelta, Wasmannia.*

7. Pheidoloid—Subtriangular; with two or three subapical teeth not all in the same plane; apex curved medially to form a tooth. Occurrence: MYRMICINAE: *Cardiocondyla,*

Carebara, Ischnomyrmex, Lophomyrmex, Mayriella, Oligomyrmex, Paedalgus, Pheidole, Trigonogaster.

8. Platythyreoid—Narrowly subtriangular; with a medial blade arising from the anterior surface; with or without medial teeth; apex curved medially to form a tooth. Occurrence: PONERINAE: *Anochetus, Bothroponera, Eubothroponera, Plathythyrea, Thaumatomyrmex.* PSEUDOMYRMECINAE: *Pseudomyrmex.*

9. Cephalotoid—Apex rounded and curved medially; no medial teeth. Occurrence: PONERINAE: *Myopias.* MYRMICINAE: *Allomerus, Anergates, Cephalotes.*

10. Attoid—Broad, short and stout; apical portion abruptly attenuated and curved medially to form a sharp-pointed apical tooth; no medial teeth. Occurrence: MYRMICINAE: *Acromyrmex, Atta, Cyphomyrmex, Mycetosoritis, Sericomyrmex, Trachymyrmex.*

11. Dinoponeroid—Narrowly subtriangular; distal portion strongly curved posteriorly; without a blade; with one or two medial teeth. Occurrence: PONERINAE: *Dinoponera, Trapeziopelta.* PSEUDOMYRMECINAE: *Pseudomyrmex.* MYRMICINAE: *Daceton.*

12. Diacammoid—Falcate; with the base dilated; with or without minute medial teeth, apex forming long a long sharp-pointed tooth. Occurrence: PONERINAE: *Brachyponera, Diacamma, Megaponera, Ophthalmopone.*

13. Tetraponeroid—Short, stout and blunt; apical tooth short and directed medially; with one lateral subapical tooth and one blunt subapical medial tooth. Occurrence: PSEUDOMYRMECINAE: *Pachysima, Tetraponera, Viticicola.*

14. Rhytidoponeroid—Basal half greatly inflated and terminating medially in a large tooth, which is directed ventrally; distal half very narrow and forming a long slender apical tooth; one or two small medial teeth. Occurrence: PONERINAE: *Rhytidoponera.* FORMICINAE: *Plagiolepis.*

15. Leptanilloid—Outer border furnished with several long slender sharp-pointed teeth; apical tooth long, slender, sharp-pointed and directed laterally. Occurrence: LEPTANILLINAE: *Leptanilla, Leptomesites.*

16. Typhlomyrmecoid—Basal half greatly dilated; distal half extremely narrow and straight, terminating in a long slender curved apical tooth. Occurrence: PONERINAE: *Typhlomyrmex.*

17. Anergatidoid—Elongate-lobose; slightly curved medially; with an apical denticle but no teeth. Occurrence: MYRMICINAE: *Anergatides.*

18. Leptogenyoid—Subconical; apex rounded; a small subapical denticle projecting posteriorly; no teeth. Occurrence: PONERINAE: *Leptogenys.*

SURFACE—In 47% of the genera all surfaces of the mandibles are smooth. In 6% one or more surfaces are roughened with both striae (including ridges or grooves) and spinules. In 13% there are striae but no spinules; 34% have spinules but no striae. Of the 19% with striae, the striae are on the anterior surface only in 4%; in 15% they are on both anterior and posterior surfaces. Of the 40% with spinules, the spinules are on the lateral surface only in one genus (*Apterostigma*), on the medial surface only in 2 genera (*Stenamma* and *Aphaenogaster*), on the posterior surface only in 4 genera, on the anterior surface only in 25% and on both anterior and posterior surfaces in 10%.

Spinules on the anterior surface are arranged in rows in 25% and isolated in 13%, those on the posterior surface are arranged in rows in 10% and isolated in 6%. On the anterior surface the spinules are coarse in 13%, minute in 24%; on the posterior surface they are coarse in 3% and minute in 9%.

Spinules are most elaborate in the genus *Gnamptogenys* where the basal ⅔ or ¾ of the anterior surface is beset with numerous spinules arranged in longitudinal rows; the spinules are mostly minute, but along and near the lateral border of the middle portion they are exceedingly long. They are also quite evolved in the Attini, where they are coarse, sharp and directed apically; their function is to hold and puncture egg shells, fungus hyphae and gongylidia.

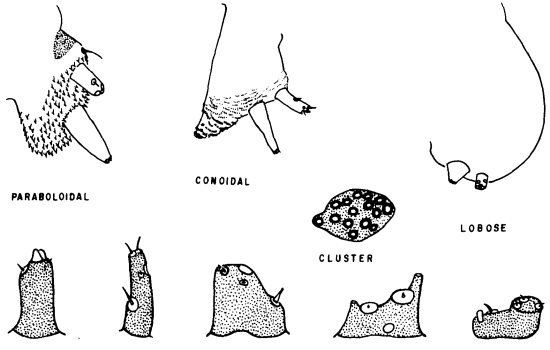


Fig. 21. Classification of maxillae, palps and galeae shapes.

Ridges are best developed in the Formicinae, where they characterize the whole subfamily (except *Myrmecorhynchus*) and where they are few to numerous on both anterior and posterior surfaces. In several genera some of the ridges bear minute spinules; in *Camponotus* most of the ridges on the posterior surface bear a comb of long spinules.

The hypothetical typical ant larva would have minute spinules arranged in rows on the anterior surface only; there would be no striae.

MAXILLAE

The rounded fleshy maxillae (Fig. 21) protrude ventrolaterally from each side of the head. In some of the Ponerinae and Myrmicinae the base of each maxilla is divided by a transverse groove into a proximal cardo and a distal stipes. In a few genera this division is emphasized by a superficial sclerotized band alongside the groove. Distally the stipes generally merges without boundary into a narrower projection, the lacinia, which we have called the apex. The lacinia is usually directed ventromedially, but in many genera it is directed medially and in a few ventrally. In many genera (23%) there is no distal narrowing; these maxillae we have described as lobose. In 34% the narrowed portion is paraboloidal (i.e., with a broadly rounded end); in 36% it is conoidal (i.e., with a blunt-pointed end). In 7% the maxillae appear to be adnate to the head; hence the above terms do not apply.

Fifty-five per cent of the genera have some part of the anterior maxillary surface spinulose. The spinules may be restricted to a small patch or, at the other extreme, may cover the entire lacinia and extend onto the stipes. In size the spinules range from minute to large; they may be arranged in rows (26%) or isolated (22%). In 40% we have found no maxillary spinules.

The only sharply defined parts of the maxilla are the palp and galea,

which are on the stipes. Typically these are two feebly sclerotized paxilliform projections, which are directed ventrolaterally; the palp is proximal, the galea distal and subapical. The galea is nearly always longer than the palp, but in *Myrmica* the two are equal, while in *Pogonomyrmex* and in *Pheidole hyatti* the galea is the shorter.

The palp is usually (59% of the genera) paxilliform (also called in our descriptions a slender cone, a subcone, a skewed peg, a cylinder, a frustum or a peg). In 10% it is papilliform (a low convexity or a low projection or a boss or a knob). In 5% it is digitiform (fingerlike). In 6 genera it is chair-shaped, while in 1 it is bootee-shaped. In 24% the palp as a protuberance is lacking but is represented by a cluster of sensilla; in 43% of these genera the sensilla are on the surface of the stipes, but in 57% the cluster is slightly elevated from the general surface.

Since the palp is a sense organ, it is furnished with sensilla. In position the sensilla may be apical, subapical, lateral or basal. In shape a sensillum is discoidal and usually bears a small spinule, but in a few it bears a long spinule; in some genera one or more sensilla may be encapsulated (with a smooth convex cap); in a few others one of the sensilla is paxilliform. The typical number (69% of the genera) of sensilla per palp is five, but 19% have four, while 12% have various other numbers (1-21).

The galea is usually (46% of the genera) digitiform, but in a considerable number (34%) it is paxilliform; in 7% it is papilliform, while in 12% it is represented only by two sensilla. In the vast majority (94% of the genera) the galea bears two apical sensilla, but 10 genera have a different number (1-7).

LABIUM

SHAPE—In most genera the labium (Fig. 22) is either a hemisphere or a short stout cylinder with a rounded ventral end; the difference probably results from different degrees of contraction at the time of preservation. A few other shapes have been reported in a few genera. In every genus, however, the labium protrudes ventrally from the posteroventral region of the head. The only clearly defined parts are the opening of the sericteries and a pair of palps.

SURFACE—In the majority of genera (78%) the anterior surface of the labium is furnished with spinules. Occasionally the spinules extend on to the lateral, ventral or posterior surfaces. In 22% the labium is without spinules. Of the 78% the spinules are abundant in 46% and sparse in 33%, minute in 63% and large in 15%, arranged in rows in 58% but isolated in 19%.

THE PALPS—The palps may be anterior or ventral or ventrolateral. Here again the difference in location may be due to difference in degree of contraction at the time of preservation.

In 38% of the genera the palp is papilliform (also called, in our descriptions, a low convexity or a low projection or a boss or a knob). But nearly as often (37%) it is paxilliform (also called a slender cone or a subcone or a skewed peg or a cylinder or a frustum or simply a peg). In only 3 genera it is digitiform (fingerlike). In 24% the palp as a projection is lacking but is represented by a cluster of sensilla on the surface of the labium.

Since the palp is a sense organ, it is furnished with sensilla. In

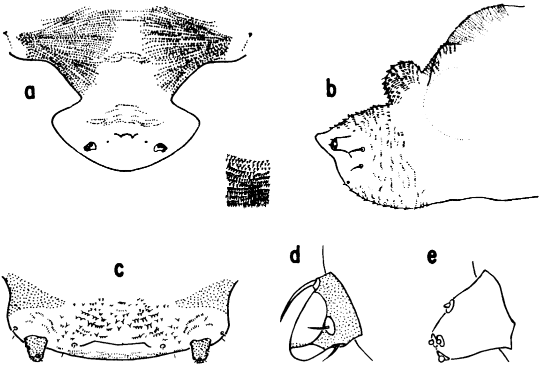


Fig. 22. a, Labium and hypopharynx in anterior view, and enlargement of spinules of hypopharynx (left dorsolateral portion); b, labium and hypopharynx in side view, labium with dorsal spinulose transverse welt (hypothetical ancestral ant larva) (*Cryptopone gilva*); c, labium with anterior surface moderately spinulose, spinules minute and isolated or in short rows (hypothetical generalized type) (*Pogonomyrmex occidentalis*); d, left palp in side view, with 5 sensilla (2 apical and encapsulated and 3 lateral and with a spinule each) (*Rhopalomastix gravis*); e, left labial palp in side view with 4 sensilla (3 apical and 1 lateral) (*Pogonomyrmex occidentalis*).

position the sensilla may be apical, subapical, lateral or basal. In shape a sensillum is discoidal and usually bears a small spinule, but in a few the spinule is long; in some genera one or more sensilla may be encapsulated (with a smooth convex cap); in a few others one of the sensilla is paxilliform. The typical number (62% of the genera) of sensilla per palp is five, but 18% have four and 11% have three, while 9% have various other numbers.

ISOLATED SENSILLUM—In many genera there is a single isolated sensillum on the surface of the labium between the palp and the opening of the sericteries. This is a minor character, but it may prove taxonomically useful in the future.

OPENING OF SERICTERIES—The opening of the sericteries is medial and either anterior or ventral. In the majority of genera (68%) it is a transverse slit. In 31% it is wide and salient; these are in the cocoon-spinning subfamilies Myrmeciinae, Ponerinae and Formicinae.

HYPOPHARYNX

We have applied this term to the portion of the pharyngeal floor immediately dorsal to the labium (Fig. 22). It is inside the mouth but

readily seen in cleaned preparations. Our interest in it stems from the fact that it is usually spinulose and therefore probably involved in the trituration of food.

Spinules are present on the hypopharynx of 70% and lacking in 30%. We have described the spinules as numerous (or dense) in 58% and as sparse in 12%; as minute in 61% and large in 9%. The spinules are arranged in rows in 69%; isolated spinules occur in only 4 genera. In nearly all (90%) Dolichoderinae and Formicinae these rows of spinules are grouped in two subtriangles, which have their bases near the midline.

SYSTEMATICS

FAMILY FORMICIDAE

HYMENOPTEROUS LARVAE—The larvae of the two suborders of Hymenoptera are so different that it is impossible to characterize the order as a whole. Michener (1953b: 993) has distinguished the larvae of the suborder Clistogastra (= Apocrita) (to which the ants belong) as follows: "Antennae and maxillary and labial palpi one-segmented to absent; (apex of abdomen not sclerotized); lacinia indistinct or absent; eye-spot absent; legs absent." To this we would add: grublike; pale-colored; head feebly or not at all sclerotized; alimentary canal closed between midgut and hindgut; not living in exposed situations but usually in plant or animal tissues or in nests.

Michener (1953b: 994) then separated the larvae of Chrysididae, Formicidae, Pompilidae, Scoliidae, Sphecidae (in part) and Vespidae from other Clistogastra by these characters: salivary opening single (slit-shaped, oval or round) or absent; maxillae each with two papillae (galea and palp); cardo separated from stipes by sclerotic line or at least by a fold (except in some ants). He did not attempt to isolate the Formicidae.

FORMICID LARVAE—Some entomologists have attempted a family description for the larvae of the Formicidae, but they have all used characters which are (1) common to Insecta (e.g., mouth parts), (2) common to Clistogastra (e.g., those mentioned above), (3) those shared with the five other families mentioned above, (4) not common to the Formicidae or (5) erroneous.

We regret to confess that after half a century of study by the senior author and twenty years by the junior author we are unable to do much better. The little that we have added is given in the following comparison, and even these characters must all be qualified to accommodate exceptions.

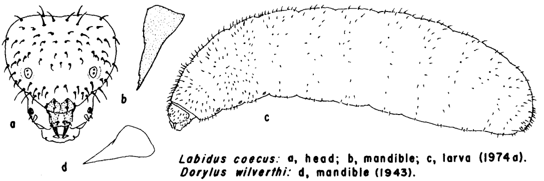
FORMICIDAE	OTHER CLISTOGASTRA
1. Antennae high on cranium (mostly at or above the middle).	1. Antennae low on cranium (below the middle—mostly at or below the lower third).
2. Thorax usually attenuated rather abruptly to form an obvious neck, but in many genera the head is applied directly to the ventral surface without a neck.	2. Thorax as stout as abdomen or reduced gradually, not forming an obvious neck.
3. Spiracles usually small and simple.	3. Spiracles usually large and complex.
4. Hairs usually abundant, and moderately long; often branched or hooked.	4. Hairs usually few, simple and minute to short.
5. Larvae never confined in cells but living in the nest chambers of the colony.	5. If social, each larva confined in a cell of wax or paper.

Our characterization of ant larvae follows: Soft, legless, translucent white (or whitish) grubs. Thirteen somites. Ten pairs of spiracles. Integument thin and delicate. Thorax usually attenuated rather abruptly to form an obvious neck, but in many genera the head is applied to the ventral surface without a neck. Hairs usually abundant and moderately long; often branched or hooked. Head small but distinct (though not always conspicuous); not sclerotized; of the same color as the body. Eyes absent. Antennae high on the cranium, mostly at or above the middle half; one-segmented; reduced to a mere discoid; usually with three sensilla each. Labrum a fleshy flap. Mandibles and pleurostoma the most sclerotized parts of the larva. Maxillae each with two one-segmented projections —palp and galea; lacinia indistinct. Labium lobose; bearing a pair of one-segmented palps and the slitlike opening of the sericteries.

LARVAE OF THE SUBFAMILIES

DORYLINAE

Profile myrmecioid. Head large, on anterior end. Leg vestiges large and conspicuous. Hairs short, unbranched and usually smooth. Antennae with 2 sensilla each. Mandibles feebly sclerotized; shape either amblyoponoid (*Aenictus, Eciton, Labidus, Neivamyrmex*) or dolichoderoid (*Cheliomyrmex, Dorylus*). [Tribes not considered.]



Labidus coecus: a, head; b, mandible; c, larva (1974a). *Dorylus wilverthi*: d, mandible (1943).

SUBFAMILY DORYLINAE

LEPTANILLINAE

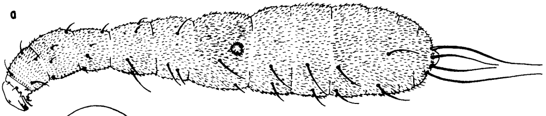
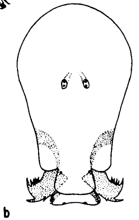
Profile leptanilloid. With a complex structure projecting anteroventrally from venter of prothorax. Only 1 pair of spiracles which is on AIII; each spiracle opening on a naked circular area. Body hairs smooth and unbranched; mostly short but a few long and flexuous. Antennae with 2 sensilla each. Mandibles leptanilloid; feebly sclerotized.

CERAPACHYINAE

Profile myrmecioid. Leg vestiges small paraboloidal papillae. Antennae with three sensilla each. Body hairs usually not simple. Mouth parts large and prominent, bearing few or no spinules. Mandibles amblyoponoid, rather feebly sclerotized. [Tribes not considered.]

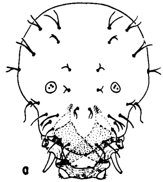
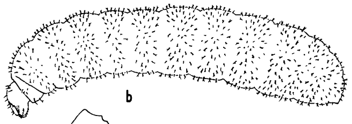
MYRMECIINAE

Profile myrmecioid. Body hairs short, moderately abundant, denticulate or smooth and unbranched. Antennae with 3 sensilla each. Head hairs usually smooth, unbranched and short. Posterior surface of labrum, basal portion of mandibles and apex of maxillae usually with large isolated spinules. Mandibles ectatommoid and heavily sclerotized. [Tribes not considered.]

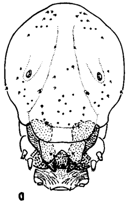
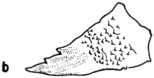
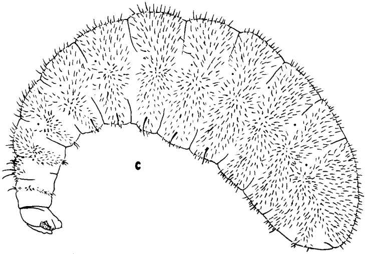

Leptanilla revelierei: a, larva; b, head; c, mandible (1965b).

SUBFAMILY LEPTANILLINAE


Cerapachys australis: a, head; b, larva; c, mandible (1973a).

SUBFAMILY CERAPACHYINAE

Myrmecia gulosa: a, head; b, mandible (1952a). *M. fulvipes:* c, larva (1971a).

SUBFAMILY MYRMECIINAE

of mandibles and spinules on maxillae, labrum and hypopharynx; in *Prenolepis* (Formicinae), which differs in position of anus, body hairs, head shape, antennal size, labial size, mandible shape, sensilla on maxillary palp and abundance of labial spinules.

HYPOTHETICAL ANCESTRAL ANT LARVA

"Ancestral" (or "primitive") should not be confused with "generalized." The opposite of "generalized" is "specialized;" the opposite of "primitive" is "derivative." One would not expect an ancestral type to be *highly* specialized. But specialization is relative and there is no reason why an ancestral type should not be somewhat specialized. Indeed with a specialization index of 23 for *Myrmecia* and 25 for *Methocha* these two genera are above the average (22) for all ant genera, while our hypothetical ancestral ant larva has a specialization index of 15.

Of all the ant larvae we have studied the larva of *Myrmecia* seems to us to be the closest approximation to the hypothetical ancestral ant larva, for the following reasons:

(1) The subfamily Myrmeciinae is generally regarded as among the most archaic living ants. It comprises only two genera, *Myrmecia* and *Nothomyrmecia*. The latter "appears to satisfy nearly all conditions demanded of an ancestral stock leading to the *Dolichoderinae* and *Formicinae*" (Brown 1954: 23). Unfortunately the larva of *Nothomyrmecia* is unknown; hence we must be content with *Myrmecia*. We are not indulging here in circular reasoning by regarding a larva as primitive, merely because its adult is primitive. On the other hand, we do not consider the larval stage as decisive in problems of taxonomy, merely as corroborative. Hence if an adult is primitive, its larva may also be regarded as primitive, unless there are compelling reasons—such as obvious adaptations—for concluding otherwise.

(2) The larva of *Myrmecia* shows many similarities to the larva of *Methocha* in the wasp family Tiphiidae, which is considered to be close to the possible ancestor of the Formicidae. *Teste* Wilson, Carpenter and Brown 1967: "*Sphecomyrma* presents a mosaic of wasplike and antlike character states. There are nevertheless enough truly antlike traits to place *Sphecomyrma* within the Formicidae, where the most similar (but still quite different) forms are the living myrmeciine *Nothomyrmecia macrops* . . . . Compared with living wasp genera, *Sphecomyrma* appears to come closest to the tiphiid genera *Methocha* (Methochinae) and *Rhagigaster* (Thynninae)."

Dr. Howard E. Evans has carefully described and figured (1965) the larva of *Methocha stygia* (Say). Furthermore, he has generously given us his material in order that we might compare it with larvae in our collection. Our description follows.

Methocha stygia (Say)—See Fig. 23. Length (through spiracles) about 10 mm. Crescentic, widest at AV, tapering rapidly to the round-pointed posterior end and more gradually to the anterior end. Anus terminal with thick anterior and posterior lips. Leg vestiges present. Thirteen differentiated somites. Ten pairs of spiracles, AI largest, T3 vestigial. Integument spinulose, the spinules minute and in short transverse rows on T1 and AX and in patches of rows on the dorsal and ventral surfaces of all somites, spinules isolated elsewhere. Body hairs about 0.01 mm long, very few, simple, fine. Head small; cranium slightly longer than broad, feebly cordate. Antennae rather large, slightly elevated and low on the head, each with three sensilla, each

TABLE 2. *Comparison of characters of* Methocha stygia *(a wasp near the putative ancestor for the family Formicidae), our imagined hypothetical ancestral ant larva and the larva of the primitive ant genus* Myrmecia, *the bulldog ant of Australia.*

CHARACTER	*Methocha stygia*	Hypothetical Ancestral	*Myrmecia*
Profile	crescentic	myrmecioid	myrmecioid
Posterior end	narrow-pointed	round-pointed	round-pointed
Anus	terminal	subterminal	subterminal
anal lips	prominent	posterior present	posterior present
Leg vestiges	large	large	large
Segmentation	13 distinct somites	13 distinct somites	10 distinct somites
Integumentary spinules	generally distributed, isolated or in rows	generally distributed, isolated or in rows	on venter of T1 and T2 (rarely generally distributed), isolated or in rows
Body hairs	few	moderately numerous	moderately numerous
shape	simple	simple	simple or denticulate-uncinate
size	minute (0.01 mm)	short	short (0.06-0.2 mm)
Head	subcordate	subcordate	subcircular or subpyriform
Antennae	large bosses	moderate	small, mounted on base
position	low on head	at midlength	at midlength
sensilla	three	three	three
Head hairs	few	few	few
size	short, about 0.01 mm	short	short, 0.01-0.12 (mostly 0.03) mm
shape	simple, fine	simple	simple or denticulate
Labrum	bilobed	bilobed	bilobed
proportion	breadth = 2X length	breadth = 2X length	breadth = 2X length
spinules on posterior surface	minute and isolated or in short rows	large and isolated	size and arrangement varied
sensilla on posterior surface	about 10	about 10	about 10
Mandibles	ectatommoid	ectatommoid	ectatommoid
sclerotization	heavy	heavy	heavy
spinules	few, small, in rows on anterior surface, on middle ½	few, large, isolated	isolated or in rows, on basal ½
teeth	3 large, 1 small	3 large	3 large

Maxillae	lobose	lobose	lobose
spinules	few, in transverse rows, on basal half	numerous, large, on apical half	apical half spinulose
palp	cone, with 5 sensilla	cone, with 5 sensilla	frustum, with 5 sensilla
galea	cone, with 2 apical sensilla	digitiform, with 2 apical sensilla	cone, with 2 apical sensilla
Labium	transversely subelliptical, with dorsal welt	transversely subelliptical, with dorsal welt	transversely subelliptical, with dorsal welt
spinules	lacking	rather large and isolated	rather large and isolated
palp	boss, with 4 sensilla	paxilliform, with 5 sensilla	frustum, with 5 sensilla
sericteries	wide and gaping, with thick lips	wide and salient	wide and salient, with 2 lateral projections
Hypopharynx	with a few transverse rows of minute spinules	spinulose, the spinules moderately numerous and rather coarse	spinules lacking

tion of anus, length and number of body hairs, position of antennae, spinules on mouth parts, sclerotization and number of teeth on mandibles, relative size of palp and galea, shape and sensilla of labial palps.

Our hypothetical ancestral ant larva differs from the larva of *Myrmecia* in the following particulars: shape of body, size and position of antennae, hair shapes on body and head, spinules on hypopharynx.

In Table 2 and Fig. 23 we compare several characters of *Myrmecia* (right-hand column) with the same characters in *Methocha* (left-hand column); in the middle column we have imagined this character for our hypothetical ancestral ant larvae.

(3) Our third reason for considering the larva of *Myrmecia* as the closest approximation to the hypothetical ancestral larva is that none of its characters shows adaptation to any limited function or habit.

(4) The larva of *Myrmecia* shows numerous similarities to those larvae in the subfamilies Ponerinae, Myrmicinae and Formicinae whose adults are considered the most primitive.

KEY TO THE MATURE ANT LARVAE IN OUR COLLECTION

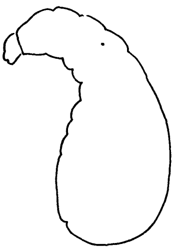
Several of the genera studied have not been included in this key for the following reasons: all our material is damaged (*Acropyga, Anergatides, Apsychomyrmex, Araucomyrmex, Calomyrmex, Dendromyrmex, Ischnomyrmex, Liometopum, Myrmicaria, Mystrium, Thaumatomyrmex, Tranopelta, Zacryptocerus*), we have only immature specimens (*Aneuretus,* *Dacetinops, Harpagoxenus, Simopelta, Technomyrmex, Triglypho-*

Acanthognathus,

thrix), or we have only semipupae (*Basiceros, Hagensia, Huberia, Hylomyrma*).

An asterisk before the name of a taxon signifies that the rubric applies to a majority of the genera in that taxon; those to which it does not apply have been keyed out earlier or later. The names of subfamilies are in capitals; those of tribes are in Roman lower case; those of genera are in italics. When a tribal name is used alone, the tribe is in the Myrmicinae; otherwise the subfamily is indicated.

PROFILE 1. POGONOMYRMECOID



POGONOMYRMECOID

Diameter greatest near middle of abdomen, decreasing gradually toward head and more rapidly toward posterior end, which is rounded; thorax more slender than abdomen and forming a neck which is curved ventrally.

1a. Body beset with tubercles .... Odontomachini and *Ponerini in PONERINAE 17

1b. Body without tubercles 2

2a. Mandibles amblyoponoid .... *Amblyopone* in PONERINAE

2b. Mandibles rhytidoponeroid .... *Rhytidoponera* in PONERINAE

2c. Mandibles dinoponeroid .... *Daceton* in Dacetini

2d. Mandibles pristomyrmecoid 3

2e. Mandibles camponotoid 4

2f. Mandibles pogonomyrmecoid 5

2g. Mandibles ectatommoid 8

3a. With anchor-tipped hairs on dorsum .... *Pristomyrmex* in Myrmecinini

3b. Without anchor-tipped hairs .... *Myrmecina* in Myrmecinini

4a. Some body hairs lanceolate; maxillae and labium without spinules .... *Messor* in Pheidolini

4b. Not as above .... *FORMICINAE 26

5a. With anchor-tipped hairs on dorsum 6

5b. Without anchor-tipped hairs 7

6a. Other body hairs short, smooth and spikelike .... *Podomyrma* in Myrmecinini

6b. Other body hairs denticulate or with bifid tip .... *Dacryon* in Myrmecinini

7a. Some body hairs half-bifid, with branches denticulate .... *Epopostruma* in Dacetini

7b. Without such hairs .... *Pogonomyrmex* in Myrmicini

8a. With anchor-tipped hairs on dorsum 9

8b. Without anchor-tipped hairs 12

9a. Anchor-tipped hairs with slender shaft and feeble hook, on lateral and ventral surfaces as well as dorsal .... *Liomyrmex* in Solenopsidini

9b. Anchor-tipped hairs with shaft and hook stout, restricted to dorsum 10

10a. Head hairs few (less than 40) .... *Tetramorium* in Tetramoriini

10b. Head hairs moderately numerous (40 or more) 11

11a. Labrum very broad (breadth 4 times length); genae bulging .... *Dilobocondyla* in Myrmecinini; ~~*Acanthognathus* in Dacetini~~

11b. Not as above .... *Myrmica* in Myrmicini and *Leptothorax* (*Mychothorax* and *Nesomyrmex*) in Leptothoracini

12a. Body hairs deeply bifid, their tip curled in opposite directions .... *Colobostruma, Clarkistruma* and *Orectognathus* in Dacetini

12b. Hairs not as above 13

13a. Head without hairs .... *Stigmatomma* in PONERINAE

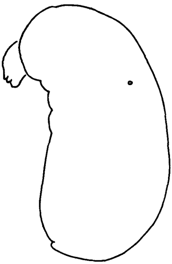
13b. Head with hairs 14

14a. Body hairs unbranched, with tip denticulate 15

14b. Body hairs unbranched, the basal half stiff and denticulate .... *Ectatomma* in PONERINAE

14c. Body hairs unbranched and smooth .... *Paraponera* in PONERINAE

14d. Most body hairs multifid, with branches smooth 16
14e. A few of dorsal body hairs denticulate, flexuous and ending in a sharp-pointed bulb .... *Eurhopalothrix* in Basicerotini
15a. Each antenna a paraboloidal knob, with 3 sensilla, each of which bears a minute spinule .... *Heteroponera* in PONERINAE
15b. Each antenna cylindrical, with 3 sensilla, each of which bears a long stout spinule .... *Gnamptogenys* in PONERINAE
16a. Cranium subpyriform in anterior view .... *Paramyrmica* in Myrmicini
16b. Cranium subhexagonal in anterior view .... *Manica* in Myrmicini
17a. Neck short and stout; abdomen short, straight and subcylindrical 18
17b. Neck long and slender; abdomen subovoidal but with ventral profile straight 19
17c. Thorax curved or bent ventrally but neck indistinct; abdomen moderately swollen 24
18a. Typical tubercle a slender subcone with hairs on its sides .... *Neoponera*
18b. Tubercles not as above .... *Bothroponera* I and II
19a. With 2 or 4 glabrous discoids on dorsum .... *Anochetus* and *Odontomachus*
19b. With 2 unpaired doorknobs on dorsum .... *Myopias*
19c. With neither discoids nor doorknobs on dorsum 20
20a. Typical tubercles spinelike 21
20b. Typical tubercles not spinelike 23
21a. Tubercles moderately numerous (96) .... *Euponera*
21b. Tubercles extremely numerous (300+) 22
22a. Mandibles ectatommoid .... *Psalidomyrmex*
22b. Mandibles pogonomyrmecoid .... *Centromyrmex*
23a. Mandibles dinoponeroid; typical tubercle a conoid .... *Dinoponera* and *Trapeziopelta*
23b. Mandibles diacammoid, with base spinulose .... *Diacamma* and *Ophthalmopone*
23c Mandibles ectatommoid .... *Bothroponera* III, *Mesoponera*, *Odontoponera*, *Pachycondyla*
23d. Mandibles leptogenyoid .... *Leptogenys*
24a. With a single doorknob or glabrous discoid on dorsum .... *Brachyponera*
24b. With 2 pairs of doorknobs on dorsum .... *Hypoponera*
24c. With 5 pairs of doorknobs on dorsum .... *Cryptopone*
24d. With 3 or 4 pairs of doorknobs on dorsum 25
25a. Head and body hairless; cranium subcordate .... *Belonopelta*
25b. Body hairs few; head hairs moderately numerous: cranium suboctagonal .... *Ponera*
26a. Short and stout; curved somewhat at anterior end; with stout neck .... *Myrmecorhynchus*
26b. Thorax and first abdominal somite forming a distinct neck, which is strongly arched ventrally; remainder of body elongate, straight, subcylindrical and rather slender 27
27a. Chiloscleres present .... Tribe Camponotini
27b. Chiloscleres lacking .... Tribes Formicini, Gesomyrmecini, Gigantiopini, Melophorini and Plagiolepidini

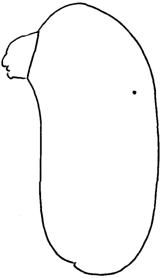


PHEIDOLOID

PROFILE 2. PHEIDOLOID

Abdomen short, stout and straight; head ventral near anterior end, mounted on a short neck, which is the prothorax; ends rounded, one more so than the other.

1a. Mandibles dolichoderoid .... *Engramma* in DOLICHODERINAE
1b. Mandibles camponotoid 2
1c. Mandibles pristomyrmecoid 3
1d. Mandibles pogonomyrmecoid 5
1e. Mandibles cephalotoid 7
1f. Mandibles pheidoloid 8
1g. Mandibles ectatommoid 9
2a. Body hairs mostly 3-5 branched, a few longer and whiplike .... *Brachymyrmex* in FORMICINAE
2b. Body hairs with tip flattened and fringed with denticles, a few tapered and denticulate and a few smooth, longer and flexuous .... *Stigmacros* in FORMICINAE
3a. With anchor-tipped hairs on dorsum .... *Macromischoides* in Leptothoracini
3b. Without anchor-tipped hairs 4
4a. Some body hairs deeply bifid, their tips curled in opposite directions. .... *Pheidologeton* in Pheidologetini
4b. Without such hairs .... *Wasmannia* in Ochetomyrmecini
5a. With anchor-tipped hairs on dorsum .... *Smithistruma* and *Strumigenys* in Dacetini
5b. Without anchor-tipped hairs 6
6a. Anterior surface of mandibles spinulose .... *Machomyrma* in Pheidolini
6b. Anterior surface of mandibles without spinules .... *Cardiocondyla* in Cardiocondylini
7a. With anchor-tipped hairs on dorsum .... *Anergates* in Solenopsidini
7b. Without anchor-tipped hairs .... *Allomerus* in Solenopsidini
8a. With anchor-tipped hairs on dorsum .... *Pheidole* in Pheidolini
8b. Without anchor-tipped hairs on dorsum .... *Pheidologetini and *Mayriella* in Meranoplini
9a. With anchor-tipped hairs on dorsum .... *Chelaner* in Solenopsidini and *Rogeria* in Leptothoracini
9b. Without anchor-tipped hairs 10
10a. Antennae in shallow pits .... *Calpytomyrmex* in Meranoplini
10b. Antennae not in pits .... *Solenopsidini and *Meranoplus* in Meranoplini



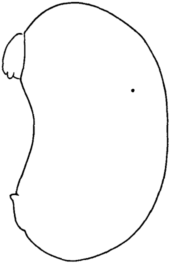
DOLICHODEROID

PROFILE 3. DOLICHODEROID

Short, stout, plump, straight or slightly curved, with both ends broadly rounded; diameter approximately equal to half the distance from labium to anus; anterior end formed by enlarged dorsum of prothorax; head ventral, near anterior end; no neck; somites indistinct.

1a. Mandibles camponotoid .... *Paratrechina* in FORMICINAE
1b. Mandibles dolichoderoid .... *DOLICHODERINAE 2
2a. Dorsal profile without bosses .... *Bothriomyrmex* and *Dolichoderus*
2b. Profile with 1 terminal or more than 1 dorsal boss 3
3a. Boss or bosses dorsal .... *Forelius, Froggattella* and *Iridomyrmex*
3b. One terminal or subterminal boss 4
4a. Boss a conoidal projection just dorsal to anus .... *Dorymyrmex*
4b. Boss a posterodorsal knob or low swelling .... *Tapinoma*

PROFILE 4. ATTOID

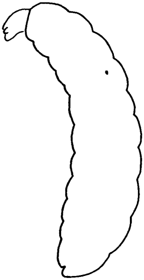


ATTOID

Similar to dolichoderoid but shorter, stouter and more curved; diameter approximately equal to distance from labium to anus (about half that distance in dolichoderoid).

1a. Mandibles attoid 2
1b. Mandibles dolichoderoid 5
2a. Body hairs stout, minute to very short (0.027-0.06 mm), some with denticulate tip 3
2b. Body hairs slender, longer (0.025-0.2 mm), with tip unbranched 4
3a. Body hairs few (about 14), minute to moderately long (0.012-0.1 mm), restricted to ventral surface .... *Mycetosoritis*
3b. Body hairs more numerous (about 40), minute to very short (0.027-0.06 mm) .... *Acromyrmex*
4a. Head hairs numerous (about 100) .... *Atta*
4b. Head hairs few (less than 40), mostly below antennal level .... *Cyphomyrmex*, *Sericomyrmex* and *Trachymyrmex*
5a. All head hairs below antennal level .... *Myrmicocrypta*
5b. Some head hairs above antennal level .... *Apterostigma*

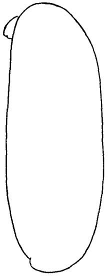
PROFILE 5. MYRMECIOID



MYRMECIOID

Elongate and rather slender; curved ventrally; without a differentiated neck; diameter diminishing only slightly from fifth abdominal somite to anterior end.

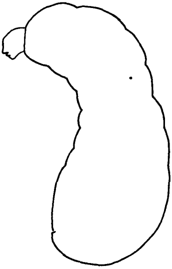
1a. Mandibles ectatommoid .... MYRMECIINAE
1b. Mandibles pogonomyrmecoid .... *Myopopone* in PONERINAE
1c. Mandibles diacammoid .... *Megaponera* in PONERINAE
1d. Mandibles amblyoponoid or dolichoderoid 2
2a. Maxillary palp bootee-shaped .... *Prionopelta* in PONERINAE
2b. Maxillary palp not bootee-shaped .... DORYLINAE and CERAPACHYINAE 3
3a. Maxillary palp represented only by scattered sensilla .... *Dorylus* in DORYLINAE
3b. Maxillary palp a conspicuous compact group of sensilla which is more or less elevated 4
4a. With a row of long (0.1-0.2 mm) uncinate hairs around each somite .... *Lioponera* in CERAPACHYINAE
4b. Body hairs all relatively short (0.025-0.14 mm) 5
5a. Mandibles dolichoderoid .... *Cheliomyrmex* in DORYLINAE
5b. Mandibles amblyoponoid 6
6a. Head hairs moderately numerous (50-100) .... *Aenictus*, *Eciton*, *Labidus* and *Neivamyrmex* in DORYLINAE
6b. Head hairs few (10-25) .... *Cerapachys*, *Eusphinctus* and *Phyracaces* in CERAPACHYINAE


CREMATOGASTROID

PROFILE 6. CREMATOGASTROID

Elongate-subelliptical; head applied to ventral surface near anterior end; no neck; somites indistinct.

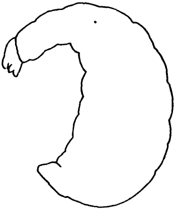
1a. With trophothylax .... PSEUDOMYRMECINAE
1b. Without trophothylax 2
2a. With long lashlike hairs on dorsum .... *Myrmelachista* in FORMICINAE
2b. With long anchor-tipped hairs on dorsum 3
2c. With long uncinate hairs on dorsum 4
3a. Mandibles cephalotoid .... *Cephalotes* in Cryptocerini
3b. Mandibles dolichoderoid .... Crematogastrini
3c. Mandibles ectatommoid .... *Xenomyrmex* in Solenopsidini; *Leptothorax* (*L.* and *Dichothorax*) and *Macromischa* in Leptothoracini; *Procrytocerus* and *Cryptocerus* in Cryptocerini
4a. Mandibles pristomyrmecoid .... *Cataulacus* in Cataulacini
4b. Mandibles dolichoderoid .... *Azteca* in DOLICHODERINAE


APHAENOGASTROID

PROFILE 7. APHAENOGASTROID

Slightly constricted at first abdominal somite, from which diameter increases gradually to middle of thorax and of abdomen; thorax arched ventrally but not forming a distinct neck; posterior end broadly rounded.

1a. Mandibles amblyoponoid .... *Onychomyrmrx* in PONERINAE
1b. Mandibles typhlomyrmecoid .... *Typhlomyrmex* in PONERINAE
1c. Mandibles ectatommoid .... *Ocymyrmex* in Ocymyrmecini
1d. Mandibles camponotoid .... *Prenolepis* in FORMICINAE
1e. Mandibles pogonomyrmecoid 2
2a. With body hairs unbranched .... *Aspididris* in Basicerotini
2b. Some body hairs half-bifid or with bifid tip .... *Stenamma* in Pheidolini
2c. Some body hairs bifid, their tips curled in opposite directions 3
2d. Some body hairs deeply bifid, their branches long and flexuous 4
2e. Some body hairs uncinate .... *Rhopalothrix* in Basicerotini
3a. Anterior surface of mandibles spinulose .... *Veromessor* in Pheidolini
3b. Anterior surface of mandibles without spinules .... *Novomessor* in Pheidolini
4a. Mandibular surfaces spinulose .... *Aphaenogaster* in Pheidolini
4b. Mandibular surfaces without spinules .... *Alistruma* and *Mesostruma* in Dacetini



PLATYTHYREOID

PROFILE 8. PLATYTHYREOID

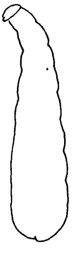
Both ends directed ventrally from a straight body; terminal somite taillike.

1a. Thorax forming a long slender neck; ventral profile jagged .... Platythreini in PONERINAE
1b. Ends curved ventrally so far that the head and tail are directed toward each other; thorax short and very stout .... Proceratiini in PONERINAE 2
2a. Body surface thickly beset with large hemispherical bosses .... *Proceratium*
2b. Body surface without bosses or with only 1 pair on prothorax .... *Discothyrea*

PROFILE 9. LEPTANILLOID

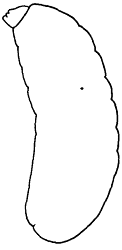
Elongate, slender and club-shaped.

1a. Mandibles leptanilloid .... LEPTANILLINAE
1b. Mandibles amblyoponoid .... *Apomyrma* in PONERINAE
1c. Mandibles pheidoloid .... *Trigonogaster* in Pheidologetini

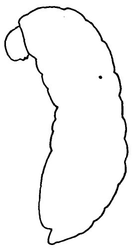


LEPTANILLOID

LEPTOMYRMECOID



OECOPHYLLOID



RHOPALOMASTIGOID

PROFILE 10. LEPTOMYRMECOID

Elongate, stout and slightly curved; diameter greatest at third and fourth abdominal somites, decreasing rapidly toward both ends; 3 posterior somites small and directed ventrally; prothorax differentiated into 2 parts, the anterior wedge-shaped (longer below) and abruptly depressed below posterior; head on anterior end with mouth parts directed anteriorly; somites distinct .... *Leptomyrmex* in DOLICHODERINAE

PROFILE 11. OECOPHYLLOID

Plump, sausage-shaped, slightly curved; diameter nearly uniform; no neck; head on anterior end .... *Oecophylla* in FORMICINAE

PROFILE 12. RHOPALOMASTIGOID

Diameter nearly uniform throughout; slightly constricted between first and second abdominal somites, body bent ventrally from this constriction; terminating posteriorly in a boss; head ventral near anterior end .... *Rhopalomastix* in Melissotarsini

BIONOMICS

DIFFERENCES IN SEX AND CASTE

We have found sex and/or caste differences among the larvae of 34 species belonging to 13 genera and representing the subfamilies Dorylinae, Pseudomyrmecinae, Myrmicinae, Dolichoderinae and Formicinae. It is noteworthy that such differences have not been detected in the less specialized subfamilies: Cerapachyinae, Myrmeciinae and Ponerinae.

In all cases we are referring to the mature larvae of the workers and sexual forms because the differences do not become distinctive until the larvae are mature. In all species studied the sexual larvae have been larger—often enormously so—than the worker larvae; the head and usually the hairs are of about the same absolute size; consequently the head of the sexual is relatively minute. In the following cases, these differences in size and proportions may not be mentioned but are neverthless to be taken for granted. In each case we have stated the nature of the differences but have not listed the differences themselves. These may be found by referring to our previous papers, which are cited by year only.

DORYLINAE

Dorylus (*Anomma*) *molesta* and *D.* (*A.*) *wilverthi* (1943). The male larva is enormous compared to the worker, which might have been expected from the difference in adult size, but it also differs markedly in shape. There may also be finer differences, but we have naturally not wished to process the two borrowed specimens.

PSEUDOMYRMECINAE

Pseudomyrmex alliodorae (1956a). There are trivial differences between sexual and worker in body shape, length of body hairs and shape of cranium. In *Ps. gracilis* (1956a), we found minor differences in body shape, length of head hairs, and shape of mandibles.

Tetraponera sp. (1956a). We noted small differences in body shape, abundance and length of hairs, size of spiracles and shape of mandibles.

MYRMICINAE

Manica mutica (1960b). The differences between sexual and worker larvae are trivial: spinulation of body, shape of cranium, number of sensilla on labrum, shape of maxillary palp. The same may be said of *M. bradleyi* (1960b): length of body hairs, number of sensilla on labrum, number and location of sensilla on maxillary palp.

Manica rubida (1972c). There are trivial differences between worker and sexual larvae in labrum and palps.

Aphaenogaster flemingi (1972c). Male and female larvae differ slightly in hairs and mandibular teeth.

Aphaenogaster longiceps (1972c). Male, female and worker larvae differ in body hairs, head hairs, hairs on labrum and mandibular teeth.

Aphaenogaster megommata (1972c). The sexual larvae differ from the worker larvae in hairs and antennal sensilla.

Pheidole dentata (1953a). There are insignificant differences between sexuals and workers in shape of hairs, integumentary spinules, shape of labrum and acuity of mandibular teeth. Except in size and proportions, the soldier larva is indistinguishable from that of the minor.

Pheidole guilelmimuelleri (1972c). Worker, female and male larvae differ considerably in shape, hairs, spinules on mouth parts and shape of maxillary palp.

Pheidole hyatti (1972c). Sexual larvae differ from worker larvae in spinules, hairs and cranial shape.

Crematogaster lineolata (1952c). The male larva differs markedly from that of the worker in shape.

Crematogaster (*Nematocrema*) *stadelmanni* (1973a). Delage-Darchen found slight differences between sexual and worker larvae.

Monomorium minimum (1955a, as *M.* sp.) Sexual and worker larvae differ in size, shape and abundance of body hairs (the former practically naked) and in size and shape of head hairs.

Solenopsis fugax (1960b). Trabert distinguished male from female sexual larvae by the length and shape of the head hairs and the shape of the mandibles.

Solenopsis molesta (1955a). Female and worker larvae differ in abundance of body hairs, the former being practically naked.

Solenopsis pergandei (1960b). Sexual and worker larvae differ only in length, shape and distribution of body hairs.

Allomerus octoarticulatus (1955a: 126). Differentiation attains what must be its apogee:

"The mature worker larva and the older sexual larva are so very different that they might be regarded as belonging to different genera (at the very least). That such is not the case is shown by the fact that we have found young sexual larvae still encased in a workerlike integument. Furthermore, a worker pupa enclosed in a worker-larval integument shows that worker larvae do not attain the definitive sexual form before pupating.

"In spite of the fact that all larvae of *Allomerus* are alike in the early instars, nevertheless, some slight differentiation does occur previous to the molt to the definitive form. The bodies of small (i.e., worker) semipupae are still about as slender and subcylindrical as are those of most of the young larvae. We have found, however, a few of the size of mature worker larvae, which differ from the latter only in being stouter, and these we have designated as 'young sexual (?)' forms."

Lophomyrmex quadrispinosus (1953c). The body and head of the sexual larvae are naked; in the worker larvae there are numerous hairs on the body and a few on the head. Also there is a slight difference in mandibular teeth.

Carebara sp. (1973a). Sexual larvae differ from worker larvae in numbers of sensilla on antennae, shape of labrum, shape of mandibles, shapes of palp and galea on maxilla and shape of palps on labium.

Tetramorium caespitum (1954b). Sexual and worker larvae differ in length of body hairs, shape of head hairs, mandibular teeth and the pattern of spinules on the hypopharynx. According to Trabert male and female larvae differ in shape of body hairs, length and shape of head hairs and the relative sizes of palps and galeae.

Wasmannia auropunctata (1954b). Female and worker larvae differ in body shape, shape and distribution of body hairs, mandibular teeth.

Cryptocerus regularis (1973b). Male larvae differ from worker larvae in hairs and cranial shape.

Strumigenys sp. (1960b). Male and worker larvae differ slightly in

body shape; in length, shape and abundance of body hairs; in shape of labium.

Atta cephalotes (1948). The female and worker larvae differ slightly in body shape.

Atta texana (1974b). Sexual larvae differ from worker larvae in shape, spinules, mandibular teeth, palps and galeae.

DOLICHODERINAE

Dolichoderus debilis (1951). Female larvae differ from worker larvae in distinctness of segmentation.

Froggattella kirbyi (1951 and 1966). The sexual larvae lack the middorsal row of bosses.

Tapinoma sessile (1951). The posterodorsal knob of the sexual larva is absolutely smaller than in the worker.

FORMICINAE

Myrmechorhynchus carteri (1970b). The female larva differs slightly from the worker in shape of body, length and shape of body hairs, shape of cranium, number and shape of head hairs, shape of labrum. The male larva differs from the female in shape, length and distribution of body hairs and in number of sensilla on posterior surface of labrum.

INTERNAL ANATOMY

In our papers on ant larvae we have dealt only briefly with internal anatomy as follows: *Eciton* 1938, *Simopelta* 1957a, *Pseudomyrmex* 1956a, *Engramma* 1951, *Camponotus* 1953d; but we have cited under the species any reference to internal anatomy that we have encountered in the literature.

The best general account of internal anatomy is still that by W. M. Wheeler (1910: 75-76) and the best figure of general internal anatomy is that of Pérez, which Wheeler repeated on p. 76.

Other illustrations of general internal anatomy: *Acantholepis*, Athias-Henriot 1947: 265 and Valentini 1951: 253; *Atopula*, Valentini 1951: 253; *Camponotus*, Tanquary 1913 Pl. LXII and Valentini 1951: 253; *Myrmica*, Tanquary 1913 Pl. LXIV; *Pheidole*, Berlese 1902: 234; *Tapinoma*, Athias-Henriot 1947: 265 and Berlese 1902: 243.

LIFE CYCLE

Along with the descriptions of ant larvae in our previous papers we have always reported the duration of the several stages of the life cycle whenever it was recorded in the literature. Originally we had hoped we might arrive at some conclusions for ants in general, but we soon realized that such hopes were vain. The influences of temperature, food supply, season and perhaps other variables, make for such great variability in the same species and even in the same colony that any statement of limits becomes almost meaningless. Almost, but not quite; at least we know that the developmental stages do not last several years, as in some beetles.

One source of confusion lies in failure to mention the semipupa (= prepupa of some authors). According to Snodgrass (1960) this stage is actually the pharate stage of the pupa. In those species which have cocoons the spinning is done by the last larval instar; the semipupa is

formed after the cocoon is finished and hence would be concealed unless the cocoon were opened.

Presumably, then, in such species the semipupa is included in the pupal duration. But the semipupa looks more like a larva than a pupa; hence, when no cocoon is spun, the semipupa is more likely to be included in the larval duration.

For whatever they are worth we give the reported limit (in days) for worker larvae by subfamily:

Dorylinae: egg 10, larva 13-16, pupa 20-21.
Ponerinae: egg 15-16, larva 22-137, pupa 31-90.
Myrmicinae: egg 6-29, larva 5-44, pupa 8-28.
Dolichoderinae: egg 12-28, larva 8-61, pupa 8-35.
Formicinae: egg 16-53, larva 7-35, pupa 14-93.

Some of the extremely long durations cited above involve overwintering stages.

The number of larval instars is known for only a few species. Bernard (1951) thought that ants usually had four, rarely five. Delage-Darchen (1972) thought that there were only three instars in *Crematogaster* (*Nematocrema*) *stadelmanni* Mayr in male, female and worker larvae. She reported (p. 269) that we had said there were four in *Aphaenogaster rudis;* Weir and Poldi had found three in *Myrmica rubra* and *Tetramorium caespitum*; Passera found five in *Plagiolepis pygmaea.* Le Masne (1953: 30) inclined to five, but was far from certain. Our observations on *Aphaenogaster rudis* (1953a) suggest that there may be six, but this was based on preserved material; it should be verified with living larvae.

In ant larvae the midgut is not connected to the hindgut. Undigested portions of the food accumulate in the midgut as the meconium. In the last moult a connection is established and the meconium is voided.

When the larva of a cocoon-spinning species is fully grown it is "buried in the earth by the workers or covered with particles of detritus, since the larva cannot spin an elliptical envelope about itself while it lies freely in the nest, but must lie in a cavity so that it can fix the threads from its sericteries to different points in an adjoining wall. The larva moves its head back and forth and lines the cavity in which it lies with a fine web of silk. As soon as this has been accomplished it is unearthed by the workers and the foreign particles adhering to the outer surface of the cocoon are carefully removed." (W. M. Wheeler 1910: 77.) When the cocoon is finished, the larva voids the meconium and its peritrophic membranes and becomes a semipupa, which resembles the larva, except that the body has become straight and rigid and there is a constriction behind the epinotal somite (AI). Through the larval cuticle may be seen the appendages and wings (if any) of the pupa, although they are still small. Next the larval skin splits down the back and is pushed to the posterior end of the cocoon where it forms a crumpled mass next to the meconium; the emerging creature is the definitive pupa.

It is not surprising that the semipupa should resemble the larva more than the pupa, since it is still enclosed in the last larval cuticle. Nevertheless, as explained above, the semipupa is no longer a larva.

In species that do not spin cocoons the mature larva simply voids the meconium and thereby becomes a semipupa. A worker grasps the meconium with its mandibles and deposits it on the refuse heap. In due time

the cuticle is shed and the semipupa become a definitive pupa. The workers dispose of the cast-off cuticle.

In our collection of ant larvae several species are represented only by semipupae. This is not a great disadvantage, because, except for body shape, the semipupa has all the external characters of the mature larva.

The fact that the last larval cuticle is retained in the cocoon gave us our clue for distinguishing the larvae of the slave-making *Polyergus* from the booty (larvae of *Formica*) in the same nest. We found a colony with cocoons containing mature pupae of *Polyergus* and removed the crumpled last larval cuticle; in spite of its poor condition, we found a few generic characters which enabled us to distinguish *Polyergus* from the already known larvae of *Formica*. Some of the mature larvae in this nest were *Formica* (recently captured booty); others showed the distinctive characters which we had found in the known crumpled cuticle of *Polyergus*. The latter we used as the basis for our description of *Polyergus* larvae.

Cocoons

All ant larvae have silk-glands (sericteries) but not all spin cocoons. In fact, the presence or absence of cocoons is used as a subfamily character: DORYLINAE—Worker pupae are enclosed in cocoons in *Labidus* and *Eciton* but naked in *Aenictus* and *Neivamyrmex;* sexual pupae are in cocoons. LEPTANILLINAE—Unknown. CERAPACHYINAE—Unknown. MYRMECIINAE—Cocoons. PONERINAE—Cocoons. PSEUDOMYRMECINAE—No cocoons. MYRMICINAE—No cocoons. ANEURETINAE—Cocoons. DOLICHODERINAE—No cocoons. FORMICINAE—Pupae usually enclosed in cocoons, but there are exceptions; the absence of cocoons is somewhat correlated with the arboricolous habit (*Colobopsis, Gesomyrmex, Oecophylla,* arboreal species of *Polyrhachis*); in certain species of *Formica* and *Lasius* cocoons and naked pupae may occur together in the same nest.

The spinning of a cocoon requires great mobility of the anterior end of the body. Hence it is not surprising that larvae with a short stout neck or no neck at all do not spin cocoons.

WEAVING—A discussion of cocoons naturally brings to mind a unique bit of insect behavior found only among ants, namely child labor. Other insect larvae can spin cocoons or webs for their own protection, but only a few species of ants are able to exploit their larvae for constructing nests for the entire colony. The species that construct nests of leaves held together by silken webs are all in the Formicinae: *Camponotus (Myrombrachys) formiciformis, C. (M.) senex, Oecophylla smaragdina, Oe. longinoda, Polyrhachis (Chariomyrma) jerdoni, P. (Cyrtomyrma)* spp., *P. (Myrmhopla) dives, P. (M.) simplex* and *P. (M.) wheeleri.* The only other known species is the dolichoderine *Technomyrmex bicolor textor,* which mixes vegetable detritus with the silk. All these species have been cited in appropriate places in our earlier papers (1951 and 1953d).

Care

The relations between ants and their brood have intrigued observers for several centuries. These relations are intimate—fully as intimate as those between the human mother and her infant, which is not surprising for in both societies utter helplessness of the young necessitates the utmost in nutricial care. The relations are much more intimate than among the

social bees and wasps, where the young (although equally helpless) are confined in cells with only the head exposed to the workers, whereas among ants all external parts and surfaces of all stages—from new-laid egg to newly eclosed callow (except pupae in those species that spin cocoons)—are exposed to the ministrations of the nurses.

For all practical purposes the brood is utterly helpless, but this is not to say that all ant larvae are inert. Many are almost incapable of movement, but those which have the anterior end attenuated into a neck of sorts are capable of considerable movement, not only of the neck but throughout the body. When hungry they thrash about and, if the workers have left food near enough, such larvae are able to find it and feed themselves. The larvae of many species are capable of a certain amount of food-trituration by their mouth parts. A few species are even capable of limited locomotion by the earthworm (or maggot) technique: the neck is extended forward, the mouth parts are set down as an anchor; then the neck is shortened or arched and the remainder of the body dragged forward.

Good general accounts of care may be found in Berlese 1925: II 845-846 (in Italian); Bischoff 1927: 384-387 (in German); Escherich 1917: 95-100 (in German); Forel 1922: III 71-75 (in French - English translation 1928:I 450-454) Le Masne 1953 (in French); Sudd 1967: 120-126; W. M. Wheeler 1910: 67-81; Wilson 1971: 35-72 and elsewhere.

Any discussion of the care of ants for their brood is divided more or less naturally into four parts: transportation, licking, feeding and minor duties.

For picking up and transporting the brood, ants use only the mandibles and tip of the gaster. Eggs and small larvae are handled in packets. Cohesion of eggs in packets is effected by sticky saliva, while that of small larvae may be due to saliva or hairs or both. Larger larvae, naked pupae and cocoons are carried singly. In most species the long axis of the brood is vertical or inclined, but in the Dorylinae, Cerapachyinae and Ponerinae they are carried horizontally beneath the body. (Photograph, Allee et al. 1949: 432 = Buchsbaum, 1948: 292-296.)

Brood may be transported for any one of three "reasons": First, safety, e.g., when a nest is opened, the workers usually remove the brood to deeper recesses of the nest with amazing speed. Second, moving the colony to a new nest. Third, homeostasis. Since most ants have no means of circulating air or of changing the temperature or humidity of any part of the formicary they do the next best (or is it better?): they move the brood to that portion of the nest where optimum conditions obtain. Eggs and young larvae require less warmth and moderate humidity; larger larvae require a more humid warmth, while pupae need drier warmth. A corollary of such differential requirements is the practice of classifying the brood. Eggs, larvae and pupae of different sizes are placed in separate piles in the same or different chambers of the nest. This practice, though general, is not invariable. Indeed the same colony may practice both segregation and mixing in the same nest or even in the same chamber.

Workers devote much of their time to licking the brood. Le Masne said (1951: 1112) they *"lèchent constamment le couvain,"* which is surely an exaggeration. At any rate, he later made (1953: 24) a partial correction by stating that they *"lèchent très fréquemment toute la surface de leurs larves."* The licking is indispensable for cleaning and cleaning

seems to be essential to health. Should any entomologist contemplate an experiment which requires the rearing of larvae in the absence of workers, he should heed Le Masne's warning before assuming the duties of myrecopedaltrix:

"Lorsqu'on élève des larves indépendamment des ouvrières, il est nécessaire de les nettoyer après les repas; mais cette opération délicate est difficile à pratiquer de manière complète; les sillons intersegmentaires conservent parfois des débris de nourriture séchée, qui constituent une des causes de mortalité pour ces larves."

FEEDING—Two aspects of the feeding of ant larvae by the workers should be considered: (a) feeding behavior and (b) food.

There are three techniques for feeding behavior: (1) The worker places the food on the flattened belly of a larva lying on its back; or when an insect fragment is placed near a larva it can feed itself by inserting its long neck; or the larva is placed on the food; in any case the larva actively comminutes the food with its own mouth parts and ingests it. (2) The food is placed in a pocket (trophothylax or praesaepium) on the ventral surface of the larva; the larva inserts its mouth parts into the pocket and helps itself to the food. (3) The worker applies its mouth to that of the larva and regurgitates from its crop liquid food which the larva imbibes. It is likely that most ants feed their very young larvae by the third technique. For some it is the only way for larvae of all ages. Most species are doubtless capable of using either (1) or (3) or both, while the Pseudomyrmecinae and Camponotini employ all three techniques.

As to the food materials, W. M. Wheeler's summary (1920: 270) is quoted below as the best available; in 50 years there has been no change in our basic knowledge, although some details have been filled in.

"The feeding of the larvae among ants exhibits a much greater diversity than in any other group of social insects. We were able to distinguish the following methods:

1. Feeding with whole insects or pieces of insects (Ponerinae, and some Myrmicinae and Formicinae);

2. With pellets made of the flesh of insects (Dorylinae);

3. With the contents of the infrabuccal pocket, either alone or with the addition of fresh insect fragments (Pseudomyrminae and possibly some Myrmicinae, such as *Cryptocerus* and *Leptothorax*). In the acacia-inhabiting species of *Pseudomyrma* portions of the Beltian bodies of the host plant are also fed to the larvae;

4. With pieces of seeds (granivorous Myrmicinae);

5. With fungus hyphae, normal or modified as 'kohlrabi,' or bromatia. (Tribe Attiini among the Myrmicinae);

6. With liquids regurgitated from the ingluvies, or crop of the worker. (Dolichoderinae, Formicinae and many Myrmicinae)."

[We would now add:

7. Eggs laid by the queen and workers are at times important items in the larval diet.]

"It is evident that the first method is the most primitive and, owing to the fact that the pieces of insects are often given to the larvae without malaxation, apparently an even more ancient form of feeding the young than we find in the social wasps. The second method, however, as employed by the Dorylinae, seems to be very much like that of the higher Vespidae. All the other methods are highly specialized and are evidently

derived secondarily from specializations in the feeding habits of the adults. This is obvious in the granivorous, fungus-growing and honey ants, which represent peculiar adaptations to life in arid or desert environments or to regions in which, during long periods of the year, insect food is very scarce. The conditions in the Pseudomyrminae are unique, owing to the development in the larvae of a special post-oral receptacle (trophothylax) for the reception of a food-pellet provided by the worker and consisting of the strigil-sweepings compacted in her infrabuccal pocket *plus* a certain amount of freshly captured and dismembered insect prey."

Every reference to food and feeding known to us has been cited (and usually quoted) in our previous articles on ant larvae. To repeat even the references here would entail undue expense. The interested reader can locate them with the aid of our bibliography.

OTHER DUTIES—These include (1) assistance in larval moulting; (2) burying larvae that are ready to spin their cocoons; (3) cleaning cocoons; (4) removing the meconium evacuated from the anus of larvae which do not spin cocoons.

TROPHALLAXIS—The term *trophallaxis* was coined by W. M. Wheeler (1918: 322) for the mutualistic exchange of food between members of an insect society, but the term was expanded to include secretions and services and to encompass (albeit incompletely) the fringes of a society (e.g., Homoptera tended by ants). The concept was further extended by W. M. Wheeler (1928: 245) and Schneirla (1957: 110) to include the exchange of stimulations of any sort. Good accounts of trophallaxis are to be found in W. M. Wheeler 1923, 1926 and 1928 and in Wilson 1971.

Lest the human observer anthropomorphize too extravagantly the altruism of the workers, he should consider trophallaxis. The workers may be so assiduous merely because they so thoroughly enjoy what they lick from their charges; the drop of saliva which the hungry larva produces (cf, human "mouth-watering") may be "worth the effort" of providing food for the larva. Ishay and Ikan (1968) reported that the liquid given to the adult oriental wasp (*Vespa orientalis*) by the larva contained sugars and amino acids which only the larvae could produce since the adults lacked the necessary proteolytic enzymes. Delage (1968: 247): "Lorsque les ouvrières absorbent une goutte de salive régurgitée par les larves, elles obtiennent, outre des protéines, une gamme de protéases extrêmement actives et, en particulier, des exopeptidases qui font défaut dans les sécrétions salivaires des ouvrières." We (Went, Wheeler and Wheeler 1972) reported that the larvae of *Manica hunteri* which had fed on radioactive fungi must have shared their food with their nurses (which had had no contact with the radioactive material) for the adult ants also showed radioactivity. In the same paper we reported that the seed coats on *Hymenoclea salsola* and *Franseria dumosa* were cut open by workers of the American harvester, *Veromessor pergandei*, only wide enough for the larvae to get their heads inside to eat the seeds. We further reported evidence that the seeds were digested inside the seed coat and the whole seeds were not extracted entire from their coat.

From the above it would seem that trophallaxis, as the exchange of food within the colony, has an importance much greater than previously recognized. Larvae may be essential for the continued healthy survival of a colony and the lack of larvae may explain the death of laboratory colonies which contain workers only.

ENEMIES OF ANT LARVAE

In all our papers on ant larvae we have cited, along with species descriptions, any reference to enemies. It would be more convenient for zoologists if we summarized all such information (together with citations) in a table, but the cost of publication would be prohibitive. Hence we give in Appendix C the taxa to which the enemies belong, the type of interaction and the genera (if cited) to which the ant hosts belong, leaving to interested parties the burden of finding the references in our earlier papers under the ant genus.

As far as known, the members of the chalcidoid family Eucharitidae parasitize ants exclusively. Twenty-two species in 14 genera have been recorded as taken with ants. Of these, 12 species in 9 genera are known to be brood parasites. The life histories of *Orasema viridis, Psilogaster fasciiventris* and *Schizaspidia tenuicornis* are known. "The two known endoparasitic members of the family, *Orasema costaricensis* W. & W. and *O. sixaolae* W. & W., attack the larvae of *Pheidole* and *Solenopsis*, respectively (Wheeler and Wheeler, 1937). The planidia were found embedded in the host bodies, with the posterior end fixed in the entrance hole in the integument and surrounded by a 'collar.' . . . It is not known whether the second and third instars are endo- or ectoparasitic, though mature larvae were free in the nest." (Clausen 1940: 227).

FOSSIL ANT LARVAE

The layman who thinks of fossils as bones and shells might be surprised that such a soft creature as an ant grub could ever be fossilized. But if a jellyfish can be fossilized; why not an ant larva? Furthermore the entomologist who has prepared whole mounts of small insects in the resin of *Abies balsamea* is not surprised to find ant larvae preserved in the resin of extinct trees.

The fossil larvae of four extinct species of ants have been recorded. Three are from the Oligocene Baltic Amber. "The larval and pupal stages of the Baltic ants were also in all respects as highly specialized and of the same structure as those of recent species. I have seen larvae and pupae of *Iridomyrmex geinitzi, I. goepperti* and *Lasius schiefferdeckeri*. The *Lasius* pupae are enclosed in cocoons, while those of *I. geinitzi* are naked, showing that the cocoon-spinning habit of the larvae had been lost in the *Dolichoderinae* as far back as the early Tertiary." (W. M. Wheeler 1914: 21.). *Iridomyrmex geinitzi* is figured on p. 87.

The fourth record (*Oecophylla leakeyi* Wilson and Taylor) is 197 larvae of various ages found in "rock" from the Lower Miocene deposits of Mfwangano Island, Lake Victoria, Kenya (Wilson and Taylor 1964).

SPECIALIZATION

To test our appraisals of degrees of specialization of taxa we have considered 46 characters (out of about 100 we use in descriptions) of 156 genera and treated them as follows: (1) Compare a character in a genus with the mode for that same character in the family (i.e., in the hypothetical typical ant larva), (2) Assign to that character a value according to the amount of its deviation—0 if the same or 1, 2 or 3. Most characters have only two values—0 and 1; all values are given in Appendix D. (3) Tabulate these values. (4) Total the values of all its characters to get the

specialization index for each genus—the larger the index, the more specialized the larvae of that genus (see Appendix E). (Our hypothetical generalized ant larva has a score of 0.) (5) Average all the generic indexes for a tribe or subfamily to get the specialization index for the higher taxon.

And after all that arithmetic what have we learned? Little that we had not already guessed during our 50 and 20 years of study of ant larvae: The most specialized ant larvae are the Leptanillinae (35). Other specialized subfamilies are Dorylinae (24), Pseudomyrmecinae (26) and Dolichoderlinae (24). The Myrmicinae are the largest and most heterogeneous subfamily; the extremes (11 and 35) and near-extremes cancel out to an average of 20. Less specialized than average are the Ponerinae (17) and Formicinae (17).

Within the larger subfamilies there are, as might be expected, great differences in specialization. Among the Ponerinae the most generalized tribe is the Ectatommini (14), while the most specialized is the Proceratiini (31). The myrmicine tribes range from the Pheidolini (13) to the Crematogastrini (35); the other more generalized tribes are Myrmicini (16) and Dacetini (15); the other more specialized are Melissotarsini (31), Cataulacini (28) and Cryptocerini (26). In the Formicinae the range is from Plagiolepidini (13) and Formicini (14) to the Camponotini (22) and Oecophyllini (24).

We did have two surprises: First, the larvae of the specialized Dacetini are relatively generalized and second, the larvae of the archaic genus *Myrmecia* are slightly more specialized than the average for the family (22). We realize that primitive is not equivalent to generalized, but we did not expect the degree of specialization we found in *Myrmecia*.

All (or nearly all) characters of ant larvae must be adaptive. So here we will consider only a few of the more obvious adaptations. The long slender neck and stout body of the larvae of the tribe Ponerini is an adaptation to feeding on insect fragments. When a worker places food on the "platter" (i.e., the flattish ventral surface of the abdomen) the larva, thanks to the neck, is able to reach all parts; at the other extreme, the immobility of a body with a dolichoderoid or crematogastroid shape precludes self-feeding. Hence these larvae must be fed by regurgitation.

The myrmecioid profile is thought to be an adaptation to the nomadic habit. The slender, elongate, subcylindrical, nearly straight larva fits readily under the body of the long-legged worker and is transported in that position. It is not surprising therefore to find this shape characterizing the larvae of the Dorylinae. But how is it to be explained in the Cerapachyinae and Myrmeciinae, which are not known to be nomadic? In Mymeciinae we regard the shape as primitive, in the Dorylinae it is, as said above, adaptive. This leaves the Cerapachyinae as the enigma.

The protuberances from the body, such as the tubercles of the Ponerini, the bosses of *Proceratium* and the knobs of some dolichoderines, certainly must have unusual functions, but they have not been determined. Four possible uses have been suggested: support, defense, attachment and trophallaxis. For a full discussion, see above and also our 1964c and 1966.

The straight subcylindrical body (without any semblance of a neck) is an obvious adaptation to life in plant cavities. We have discussed this below and in 1954c.

The most specialized hair-shape is anchor-tipped, which is found in 28 genera of Myrmicinae. In addition to facilitating clumping this type

is ideally suited for suspending the larva on the wall of the chamber. We have already discussed this under functions of hairs.

The most specialized mandible-shape is attoid, which is found only in the Attini. See above under mandibles (spinules).

The most extraordinary adaptation is the "feed bag" or trophothylax of pseudomyrmecine larvae. It is unique among ants and also (as far as we know) among insects. We have discussed it fully in 1956a. An analogous but less specialized structure is the praesaepium in the formicine tribe Camponotini. We have discussed this in 1953d (p. 180 and 189) and 1970b (p. 650). A larva with a trophothylax could be hung on a wall of the nest and could feed without spilling but a larva with a praesaepium must lie on its back to feed.

Concerning the possible functions of the most specialized of larval structures we will not even hazard a guess: the mandibles, spiracles and prothoracic protuberance of leptanilline larvae. We sometimes think that if there were a paradise for myrmecologists, we would elect the part thereof where Leptanillinae are common (is there such on earth?) and spend eternity studying them in the field and in observation nests. (It is more likely however, that we would spend an eon in a purgatory trying to read the papers of a certain British myrmecologist and then be consigned for all eternity to a myrmecological inferno where we would be forced to study the larvae of the Stygian species of *Lasius*).

CONVERGENCE

The crematogastroid body profile affords a beautiful example of convergence. It is shared by larvae in ten genera representing four subfamilies: *Crematogaster, Leptothorax* (*s. str.*), *Macromischa* and *Xenomyrmex* in the Myrmicinae; all genera in the Pseudomyrmecinae (*Pachysima, Pseudomyrmex, Tetraponera, Viticicola*); *Azteca* in the Dolichoderinae; *Myrmelachista* in the Formicinae.

The crematogastroid shape is an adaptation to life in plant cavities, particularly tubular cavities of small bore. "A long larva parked parallel and close to the wall would be less of a traffic hazard than a shorter larva parked crosswise or obliquely" (1954c: 149).

Many species in the formicine tribe Camponotini inhabit wood. The larvae of this tribe are not crematogastroid but they can achieve that form by pressing the short, stout, strongly curled neck against the elongate subcylindrical body.

The myrmecioid profile of the nomadic ponerine genus *Megaponera* is convergent to the myrmecioid profile of the Dorylinae—presumably an adaptation to transportation under the body of the long-legged worker.

TAXONOMIC CONCLUSIONS

We cannot foresee any practical value for the study of ant larvae. They do no damage in their own right, as do the larvae of Coleoptera and Lepidoptera. Furthermore, being social insects, ant larvae are never found alone but always with their workers; hence identification is no such problem as it is with larvae that live alone, e.g., Coleoptera, Lepidoptera, Symphyta and mosquitoes.

Very limited utility for myrmecologists is afforded in the following cases:

(1) To detect contamination. When two colonies of ants belonging to different genera are found under the same stone or in the same rotten log, their broods, although previously well separated, may get mixed in collecting. It might be possible to distinguish the larvae with the aid of our keys. We have rejected several samples contributed by other myrmecologists, because we knew that the larvae could not possibly belong to the same genus as the workers.

(2) To distinguish brood from prey of army ants. The late Dr. J. W. Chapman wondered whether he might have the sexual larva of *Aenictus;* we were able to assure him that it was the larva of *Diacamma.* Recently Mr. R. S. Baldridge has been studying the prey of *Neivamyrmex nigrescens* in Texas. We were able to identify the larval booty he sent us as mostly *Pheidole* and *Paratrechina.*

(3) To distinguish parasite and host larvae in mixed colonies. We had no difficulty with *Anergates* vs. *Tetramorium,* but *Polyergus* vs. *Formica* required some detective work (see above under "Life Cycle" and 1968: 214).

If our studies of ant larvae have any fundamental importance it will reside in the broader aspects of taxonomy. Our latter-day systematists have repeatedly stated that classifications should ultimately be based on *all* characters of organisms—chemical, physiological, ecological, ethological and developmental as well as anatomical. So we offer our work in partial fulfillment of the developmental requirement.

It is quite obvious that entirely different forces of natural selection are affecting the mature worker ants, which build the nest, go out to forage for food and bring it back to feed nest-mates and the larvae, and those forces affecting the larvae. The larvae are usually cared for underground under as nearly optimum conditions of temperature and humidity as the nest provides. The chief function of the larval stage, so far as we know now—is to utilize the provender as efficiently as possible, to grow and to molt repeatedly until it reaches mature size and finally emerges from a pupal form as a worker, soldier or queen (from fertilized eggs) or male (from unfertilized eggs).

There, of course, remains the unsolved—and perhaps unsolvable—problem of how much weight to give to larval characters. When larvae are better known, systematists may be able to use larval characters to help separate taxa, but for the practicing field taxonomist the adult structures will probably still be used for the identification of taxa.

The first use of larvae in ant taxonomy was Emery's 1899 classic. He described and figured the larvae of *Tetraponera* (called *Sima*) and *Pseudomyrmex* (called *Pseudomyrma*) laying great stress on "antennal rudiments", the presence of these rudiments and the hypocephaly of the larval body to help define a new subfamily Pseudomyrminae (now called Pseudomyrmecinae). He could not have known at that time that antennae are universal among ant larvae. Furthermore he did not mention the trophothylax.

But Emery backslid: In the "Genera Insectorum" (1921) he placed the pseudomyrmecines in the tribe Pseudomyrmini of section Promyrmicinae in the subfamily Myrmicinae. As one of the tribal characters he used (p. 21) "Larves hypocéphales."

Meanwhile W. M. Wheeler (1920: 53) again separated the pseudomyrmecines as the subfamily Pseudomyrminae, using the unique tropho-

thylax as one of the subfamilial characters. In 1922, when he characterized the subfamily, he devoted two-thirds of a page to larval characters.

In 1902 (p. 185-187) W. M. Wheeler wrote: "While Emery and Forel agree in regarding the [supertribe] Cerapachyinae as the most primitive of Formicidae, they hold very different opinions concerning the subfamily to which the group should be assigned. Emery . . . , who emphasizes morphological characters, regards the Cerapachyinae as veritable Dorylinae, while Forel . . . , who is inclined to lay considerable stress on ethological characters, maintains that these ants are true Ponerinae." The larvae of Cerapachyinae were then unknown, but Wheeler thought that "the larval characters would have little weight in solving the problem under consideration." Ironically it was Wheeler himself who solved it by describing (1903) the larva of *Cerapachys augustae*. "What light," asked Wheeler (p. 208-209), "do these few observations, together with those recorded in my previous paper, shed on the affinities of the Cerapachyi to the Ponerinae on the one hand and the Dorylinae on the other? . . . The following characters [of *Cerapachys augustae*] are common to both Dorylinae and Ponerinae: 1. The method of carrying the larvae is common to forms like Eciton and Leptogenys. 2. The larva is intermediate between that of Eciton and Stigmatomma. It is covered with shorter, less flexuous, and less abundant hairs than the latter and in these particulars resembles the larvae of Eciton." Emery (1904: 115) thought that the larva of *Cerapachys* preserved "completely the doryline type by its slender form, almost cylindrical, which contrasts vividly with the squat and paunchy form of the larvae of Ponerinae."

Emery in 1904 (p. 116) divided the Ponerinae into a relatively primitive group, whose males have robust triangular mandibles and whose larvae do not have piligerous tubercles ("Myrmecii, Amblyoponii, Ectatommii, Proceratii and Platythyrei"), and all the other Ponerinae, whose males have reduced mandibles and whose larvae are tuberculate.

In the "Genera Insectorum" (1911: 4) Emery divided the subfamily Ponerinae into three sections: Prodorylinae (=the present subfamily Cerapachyinae)—"Larves uniformément poilues, sans tubercules piligères;" Proponerinae—"Larves uniformément poilues, sans tubercules piligères;" Euponerinae—"Larves pourvues de tubercules piligères." Is this dichotomy of the Ponerinae still valid and useful? It is not particularly useful, since tribes adequately take care of the interval between subfamily and genus. It is valid only if a few exceptions are allowed. Without knowing the larvae Emery placed *Thaumatomyrmex, Proceratium* and *Plathythyrea* in the Proponerinae and *Onychomyrmex* and *Megaponera* in the Euponerinae. We now know that the first three have tubercles while the latter two do not. But what is really remarkable about Emery's classification is that the larvae of only nine genera were known to him—six tuberculate and three nontuberculate. In our study of the larvae of 41 ponerine genera we have found only the above five that do not conform to his sections.

In 1920 W. M. Wheeler removed the tribe Cerapachyini from the Ponerinae and established it as a separate subfamily (Cerapachyinae) using larval characters as partial justification. In 1922 when he characterized the subfamily he included larval characters (p. 52).

In 1923 (p. 335) W. M. Wheeler separated the tribe Leptanillini from

the Dorylinae and raised it to subfamilial rank (Leptanillinae), using the then unpublished study by G. C. Wheeler (1928) as supporting evidence.

Wheeler (1900: 65) used larval characters in rejecting the *subfamily* Amblyoponinae:

> "It would seem, therefore, that there are no very cogent reasons for adopting the subfamily Amblyoponinae, so far as characters drawn from the adult structure are concerned. The habits of *Stigmatomma,* as I have shown, are essentially the same as those of the Ponerinae, so that there exist no ecological grounds for accepting Forel's suggestion. The larva, however, seems to me to show very clearly that there is a greater gap between the Amblyoponii as a tribe of Ponerinae, and the tribes Ponerii and Odontomachii, than between the two last-mentioned groups. It must be remembered, however, that the larvae of two tribes of Ponerinae, the Australian Myrmecii and the cosmopolitan Ectatommii, have not been described, and that when these are known the striking differences between the Amblyoponii and the Ponerii may be reconciled. If, as Emery suggests, the Myrmicinae are descended from the Ponerinae, it is obvious from a study of the larvae that the former subfamily must have come from forms with larvae like the Amblyoponii, a group which in other respects also is generally regarded as very primitive."

In his revision of the ponerine tribe Ectatommini, Brown (1958: 179) stated that our "larval findings agree in most respects at the generic level with the new classification adopted here." But we have disagreed vigorously (1971b: 1213) with his inclusion of *Proceratium* and *Discothyrea* in this tribe.

Brown, Gotwald and Lévieux (1970: 274) have used larval characters to confirm the placing of a new ponerine genus *Apomyrma* in the tribe Amblyoponini.

W. M. Wheeler (1922) used larval differences in support of his separation of *Bothroponera* from *Pachydondyla* and restoring it to generic rank.

Taylor (1967: 5, 10, 13, 20) used larval characters (among others) in separating *Hypoponera* from *Ponera.*

Ettershank (1966: 161) used larval characters as an aid in his generic revision of the Myrmicinae related to *Solenopsis* and *Pheidologeton.*

Cole (1968: 29) used larval characters in partial justification of his retention of *Ephebomyrmex* as a subgenus of *Pogonomyrmex.*

The controversy between Forel (1911) and Emery (1912) over the placement of *Metapone* involved larval characters. Forel placed it in the Ponerinae, Emery (and subsequently W. M. Wheeler 1919) in the Myrmicinae. (See 1953b: 186.)

Kempf (1959: 393): "The morphological distinctness of the imaginal stages and the distribution of the species may even suggest to accord *Nesomyrmex* full generic status. The larvae, however, are quite close to the holarctic subgenus *Leptothorax* s. str., according to G. C. & J. Wheeler (1955), who studied those of *echinatinodis.*"

Bernard (1948: 179-180) concluded that *Atopula* belonged in the tribe Leptothoracini rather than in the Myrmecinini partly on account of larval characters.

Bernard (1955: 279): "Si les ouvrières [d'*Epixenus*] amènent à le rapprocher étroitement de *Monomorium*, les larves s'éloignent de la tribu des *Solenopsidini* et peuvent être comparées à celles des *Leptothoracini*, sauf pour la pilosité." Judging from Bernard's figure (p. 278) we agree with Ettershank (1966), who synonymized *Epixenus* into *Monomorium*, which is in the tribe Solenopsidini.

Emery (1922) expressed grave doubts when he placed *Apsychomyrmex* in the Leptothoracini. On the basis of a single damaged semipupa we concluded (1955b: 29) that the larva of *A. myops* resembles the larvae of the Myrmecinini more closely than those of the Leptothoracini.

Brown and Wilson (1959: 290) : "*Daceton* possesses, in addition to its truly primitive features, characters that appear to represent significant specializations away from the main line of dacetine evolution, viz., in sculpturing, worker polymorphism, cephalic articulation, and larval morphology (see Brown, 1953a: and Wheeler and Wheeler, 1954)."

Wilson, Eisner, Wheeler and Wheeler (1956) used larval characters in support of their removal of the tribe Aneuretini from the Dolichoderinae and elevating it to subfamily rank—Aneuretinae.

W. M. Wheeler (1922: 191) employed larval characters (among others) in separating *Gigantiops* out of the tribe Oecophyllini and establishing it in a separate tribe Gigantiopini. Our 1953d study supported the separation. Kempf and Lenko (1968: 212-213) used our findings in a further confirmation.

Larval characters have been included in the characterizations of the subfamilies of Formicidae by W. M. Wheeler (1922), Bernard (1951) and G. C. and J. Wheeler (1972a).

LARVAL CLASSIFICATION VS. ADULT CLASSIFICATION—Larval classification is concordant with adult classification in the subfamilies Dorylinae, Leptanillinae, Cerapachyinae, Myrmeciinae, Pseudomyrmecinae, Aneuretinae and Dolichoderinae (except *Azteca*); in the ponerine tribes Platythyreini, Typhlomyrmecini, Ectatommini, Proceratiini, Ponerini (except *Megaponera*), Thaumatomyrmecini and Odontomachini; in the myrmicine tribes Crematogastrini, Ocymyrmecini, Cataulacini, Cryptocerini and Attini. In 1970b we rearranged into tribes the genera of Formicinae so that they would be concordant with larval classification.

Larval and adult classifications are discordant in the ponerine tribe Amblyoponini and in all myrmicine tribes except those listed in the preceeding paragraph.

Larval classification supports the following changes since the "Genera Insectorum" (1910-1925):

1. The establishment of the subfamilies Leptanillinae, Cerapachyinae, Myrmeciinae, Pseudomyrmecinae and Aneuretinae.

2. In the subfamily Ponerinae: Brown's (1958) combining of *Chalcoponera* into *Rhytidoponera*; Brown's (1958) inclusion of *Paraponera* in the Ectatommini and his reinstating of *Heteroponera* (including *Paranomopone*) also in the Ectatommini; Brown's (1958) combining *Emeryella* and the subgenera *Parectatomma, Poneracantha* and *Gnamptogenys* of *Ectatomma* into the genus *Gnamptogenys;* the transfer of *Euponera* (*Trachymesopus*) *gilva* to *Cryptopone* (Brown 1963): the raising of subgenera *Mesoponera* and *Brachyponera* to generic rank (Wheeler and Wheeler 1971c); Brown's (1963) transfer of *Leptogenys* to the Ponerini

and the abolition of the tribe Leptogenyini; W. M. Wheeler's (1922) raising *Bothroponera* and *Hagensia* to generic rank.

3. In the subfamily Myrmicinae: the raising of *Manica* to generic rank (see Wheeler and Wheeler 1970); the separation of the Basicerotini from the Dacetini (Brown 1949, Wheeler and Wheeler 1954d); the separation of *Chelaner* from *Monomorium* (Ettershank 1966).

4. In 1970b we proposed a new tribal classification for the subfamily Formicinae which supplemented adult characters with larval characters. (Our scheme differed from both W. M. Wheeler's 1922 and Emery's 1925 classification: see below.)

Larval classification does not support the following changes:

1. Ponerinae: Brown's (1960) composition of the tribe Amblyoponini; his combining *Stigmatomma* into *Amblyopone*; Brown's (1958) combining the Proceratiini into the Ectatommini. Brown's (1973: 182) combining *Myopias* with *Pachycondyla;* the larvae of these genera are more different than are those of *Pachycondyla* and, say, *Odontomachus* (which he did not combine). (See our 1952a and 1971b.) In the same paper (page 179) he combined *Bothroponera* with *Pachycondyla;* on the basis of larval differences we would take the opposite course (1971c)—split *Bothroponera* into three genera, none of which would combine with *Pachycondyla.*

2. Myrmicinae: the separation of *Smithistruma* from *Strumigenys* (see Wheeler and Wheeler 1954d: 120).

3. Formicinae: as stated above, we found so many discordances between our larval classification and Emery's and W. M. Wheeler's schemes, that we revised the grouping of genera into tribes using both larval and adult characters. See 1970b.

ACKNOWLEDGMENTS

We are grateful for many helpful suggestions from the reviewers: Dr. W. L. Brown, Jr., Dr. H. E. Evans, Dr. D. R. Smith and Mr. G. C. Steyskal. We are deeply grateful to the editor, Dr. Lloyd Knutson, for his careful editing and his valuable advice. Many entomologists have contributed larvae to our collection. All have been duly acknowledged in our previous publications, but our special thanks for massive contributions go to Dr. W. L. Brown, Jr., of Cornell University and Rev. B. B. Lowery of Norwood, South Australia. Finally we acknowledge our deep indebtedness to Dr. Frits W. Went and Dr. Peter R. Morrison of our own Laboratory for assistance and encouragement in many ways.

APPENDICES

A. TAXONOMIC BIBLIOGRAPHY OF OUR PUBLICATIONS ON ANT LARVAE

GENERAL

1938. Are ant larvae apodous? Psyche 45: 139-145.

1960a. Techniques for the study of ant larvae. Psyche 67: 87-94

1965a. History of myrmecopedology. Bull. Entomol. Soc. Amer. 11: 85.

1972a. The subfamilies of Formicidae. Proc. Entomol. Soc. Washington 74: 35-45, 75: 378.

1972b. Facsimile reprint and translation of "Intorno alle larve di alcune formiche" by Carlo Emery, Memoria della R. Accademia della Scienze dell'Istituto de Bologna, Series V, Volume VIII, 10 p., 2 pl., 1899. Desert Research Institute, University of Nevada System, Reno, Nevada, 24 p.

DORYLINAE

1943. The larvae of the army ants. Ann. Entomol. Soc. Amer. 36: 319-332.

1964a. The ant larvae of the subfamily Dorylinae: supplement. Proc. Entomol. Soc. Washington 66: 129-137.

1974a. Ant larvae of the subfamily Dorylinae: second supplement. J. Kansas Entomol. Soc. 47: 166-172.

LEPTANILLINAE

1928. The larva of *Leptanilla*. Psyche 35: 85-91.
1965b. The ant larvae of the subfamily Leptanillinae. Psyche 72: 24-34.

CERAPACHYINAE

1950. Ant larvae of the subfamily Cerapachyinae. Psyche 57: 102-113.
1964b. The ant larvae of the subfamily Cerapachyinae: supplement. Proc. Entomol. Soc. Washington 66: 65-71.
1973a. Supplementary studies on ant larvae: Cerapachyinae, Pseudomyrmecinae and Myrmicinae. Psyche 80: 204-211.

MYRMECIINAE

1952a. [See below under Ponerinae.]
1971a. Ant larvae of the subfamily Myrmeciinae. Pan-Pacific Entomol. 47: 245-256.

PONERINAE

1952a. The ant larvae of the subfamily Ponerinae. Amer. Midland Natur. 48: 111-144, 604-672.
1957a. The larva of *Simopelta*. Proc. Entomol. Soc. Washington 59: 191-194, 207.
1964c. The ant larvae of the subfamily Ponerinae: supplement. Ann. Entomol. Soc. Amer. 57: 443-462.
1970a. The larva of *Apomyrma*. Psyche 77: 276-279.
1971b. Ant larvae of the subfamily Ponerinae: second supplement. Ann. Entomol. Soc. Amer. 64: 1197-1217.
1971c. The larvae of the ant genus *Bothroponera*. Proc. Entomol. Soc. Washington 73: 386-394.
1974b. Ant larvae of the subfamily Ponerinae: third supplement. Proc. Entomol. Soc. Washington 76: 278-281.

PSEUDOMYRMECINAE

1956a. The ant larvae of the subfamily Pseudomyrmecinae. Ann. Entomol. Soc. Amer. 49: 374-398.
1973a. [See above under Cerapachyinae.]

MYRMICINAE

1960b. Supplementary studies on the larvae of the Myrmicinae. Proc. Entomol. Soc. Washington 62: 1-32.
1960c. The ant larvae of the subfamily Myrmicinae. Ann. Entomol. Soc. Amer. 53: 98-110.
1973a. [See above under Cerapachyinae.]

1. Myrmicini

1952b. The ant larvae of the myrmicine tribe Myrmicini. Psyche 59: 105-125.
1959. The larva of *Paramyrmica*. J. Tennessee Acad. Sci. 34: 219-220.
1960b. [See above under Myrmicinae.]
1972c. Ant larvae of the subfamily Myrmicinae: second supplement on the tribes Myrmicini and Pheidolini. J. Georgia Entomol. Soc. 7: 233-246.

2. Pheidolini

1953a. The ant larvae of the myrmicine tribe Pheidolini. Proc. Entomol. Soc. Washington 55: 49-84.
1956b. *Veromessor lobognathus* in North Dakota. Psyche 63: 140-145.
1960b. [See above under Myrmicinae.]
1972c. [See above under Tribe 1.]

3. Melissotarsini

1953b. The ant larvae of the myrmicine tribes Melissotarsini, Metaponini, Myrmicariini, and Cardiocondylini. J. Washington Acad. Sci. 43: 185-189.

4. Metaponini

1953b. [See above under Tribe 3.]

6. Myrmicariini

1953b. [See above under Tribe 3.]
1960b. [See above under Myrmicinae.]

7. Cardiocondylini

1953b. [See above under Tribe 3.]
1973b. The ant larvae of six tribes: second supplement. J. Georgia Entomol. Soc. 8: 27-39.

8. Crematogastrini

1952c. The ant larvae of the myrmicine tribe Crematogastrini. J. Washington Acad. Sci. 42: 248-262.
1960b. [See above under Myrmicinae.]
1973b. [See above under Tribe 7.]

9. Solenopsidini

1935. The larva of *Allomerus*. Psyche 42: 92-98.
1955a. The ant larvae of the myrmicine tribe Solenopsidini. Amer. Midland Natur. 54: 119-141.
1960b. [See above under Myrmicinae.]
1973b. [See above under Tribe 7.]

10. Pheidologetini

1953c. The ant larvae of the myrmicine tribe Pheidologetini. Psyche 60: 129-147.
1960b. [See above under Myrmicinae.]
1973b. [See above under Tribe 7.]

11. Myrmecinini

1954a. The ant larvae of the myrmicine tribe Myrmecinini. Proc. Entomol. Soc. Washington 56: 126-138.
1960b. [See above under Myrmicinae.]
1973b. [See above under Tribe 7.]

12. Meranoplini

1954b. The ant larvae of the myrmicine tribes Meranoplini, Ochetomyrmicini and Tetramoriini. Amer. Midland Natur. 52: 443-452.
1973b. [See above under Tribe 7.]

13. Leptothoracini

1955b. The ant larvae of the myrmicine tribe Leptothoracini. Ann. Entomol. Soc. Amer. 48: 17-29.
1957b. The larva of the ant genus *Dacetinops* Brown and Wilson. Breviora Mus. Comp. Zool. Harvard. No. 78: 4 p.
1960b. [See above under Myrmicinae.]
1973c. Ant larvae of four tribes: second supplement. Psyche 80: 70-82.

14. Ocymyrmecini

1973c. [See above under Tribe 13.]

15. Tetramoriini

1954b. [See above under Tribe 12.]
1960b. [See above under Myrmicinae.]
1973c. [See above under Tribe 13.]

16. Ochetomyrmecini

1954b. [See above under Tribe 12.]

17. Cataulacini

1954c. The ant larvae of the myrmicine tribes Cataulacini and Cephalotini. J. Washington Acad. Sci. 44: 149-157.

18. Cryptocerini

1954c. [See above under Tribe 17.]
1973c. [See above under Tribe 13.]

19. Basicerotini

1954d. The ant larvae of the myrmicine tribes Basicerotini and Dacetini. Psyche 61: 111-145.
1960b. [See above under Myrmicinae.]
1973d. The ant larvae of the tribes Basicerotini and Dacetini: second supplement. Pan-Pacific Entomol. 49: 207-214.

20. Dacetini

1954d. [See above under Tribe 19.]
1960b. [See above under Myrmicinae.]
1969. The larva of *Acanthognathus*. Psyche 76: 110-113.
1973d. [See above under Tribe 19.]

21. Attini

1948. The larvae of the fungus-growing ants. Amer. Midland Natur. 40: 664-689.

1960b. [See above under Myrmicinae.]

1974c. Ant larvae of the myrmicine tribe Attini: second supplement. Proc. Entomol. Soc. Washington 76: 76-81.

ANEURETINAE

1956c. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. Comp. Zool. Harvard 115: 81-99. [With E. O. Wilson and T. Eisner.]

DOLICHODERINAE

1951. The ant larvae of the subfamily Dolichoderinae. Proc. Entomol. Soc. Washington 53: 169-210.

1966. The ant larvae of the subfamily Dolichoderinae: supplement. Ann. Entomol. Soc. Amer. 59: 726-732.

1973e. Ant larvae of the subfamily Dolichoderinae: second supplement. Pan-Pacific Entomol. 49: 396-401.

FORMICINAE

1953d. The ant larvae of the subfamily Formicinae. Ann. Entomol. Soc. Amer. 46: 126-171, 175-217.

1968. The ant larvae of the subfamily Formicinae: supplement. Ann. Entomol. Soc. Amer. 61: 205-222.

1970b. Ant larvae of the subfamily Formicinae: second supplement. Ann. Entomol. Soc. Amer. 63: 648-656.

1974d. Ant larvae of the subfamily Formicinae: third supplement. J. Georgia Entomol. Soc. 9: 59-64.

B. MATERIAL STUDIED

(= TAXA OF ANT LARVAE IN OUR COLLECTION)

DORYLINAE

Aenictus: *aratus* Forel, *laeviceps* F. Smith, *martini* Forel, *turneri* Forel
Cheliomyrmex: *megalonyx* W. M. Wheeler
Dorylus (*Anomma*): *nigricans* Illiger, *wilverthi* Emery
Eciton: *burchelli* (Westwood), *hamatum* (Fabricius), *rapax* F. Smith, *vagans* (Olivier)
Labidus: *coecus* (Latreille)
Neivamyrmex: *pilosus* (F. Smith), *nigrescens* (Cresson), *sumichrasti* (Norton)

LEPTANILLINAE

Leptanilla: *revelierei sardoa* Emery, *swanni* W. M. Wheeler
Leptomesites:*escheri* Kutter

CERAPACHYINAE

Cerapachys: *australis* Forel, *crypta* Mann, *opacus* Emery, 1 unidentified species
Eusphinctus: *steinheili* Forel
Lioponera: *luzuriagae* W. M. Wheeler & Chapman
Phyracaces: *elegans* W. M. Wheeler, *ficosus* W. M. Wheeler, *larvatus* W. M. Wheeler, *senescens* W. M. Wheeler

MYRMECIINAE

Myrmecia: *arnoldi* Clark, *brevinoda* Forel, *chasei* Forel, *clarki* Crawley, *comata* Clark, *dixoni* Clark, *elegans* Clark, *forceps* Roger, *forficata* (Fabricius), *fucosa* Clark, *fulvipes* Roger, *gracilis* Emery, *gratiosa* Clark, *gulosa* (Fabricius), *harderi* Forel, *lucida* Forel, *murina* Clark, *michaelseni* Forel, *nigrocincta* F. Smith, *picta* F. Smith, *piliventris* F. Smith, *pilosula* F. Smith, *pyriformis* F. Smith, *simillima* F. Smith, *swalei* Crawley, *tepperi* Emery, *urens* Lowne, *varians* Mayr, *vindex* Clark, *wilsoni* Clark

PONERINAE

1. Amblyoponini

Amblyopone: *australis* Erichson, *longidens* Forel
Apomyrma: *stygia* Brown, Gotwald & Lévieux

Myopopone: *castanea* (F. Smith)
Mystrium: *camillae* Emery
Onychomyrmex: *hedleyi* Emery, *mjobergi* Forel
Prinonopelta: *modesta* Forel, *opaca* Emery, *punctulata* Mayr
Stigmatomma: *pallipes* (Haldeman)

2. Platythyreini

Eubothroponera: *tasmaniensis* Forel
Platythyrea: *australis* Forel, *cribrinodis* (Gerstaecker), *incerta* Emery, *inermis* Forel

3. Typhlomyrmecini

Typhlomyrmex: *pusillus* Emery, *robustus* Emery

4. Ectatommini

Ectatomma: *quadridens* (Fabricius), *ruidum* Roger, *tuberculatum* (Olivier)
Gnamptogenys: *aculeaticoxae* (Santschi), *bispinosa* (Emery), *bisulca* Brown & Kempf, *hartmanni* (W. M. Wheeler), *menadensis* (Mayr), *mordax* (F. Smith), *regularis* (Mayr), *schmitti* (Forel), *striatula* (Mayr), *strigata* (Norton), *tortuolosa* (F. Smith), *wheeleri* (Santschi), 3 unidentified species
Heteroponera: *imbellis* (Emery), *inca* Brown, *relicta* (W. M. Wheeler)
Paraponera: *clavata* (Fabricius)
Rhytidoponera: *aspera* (Roger), *cerastes* Crawley, *chalybaea* Emery, *convexa* Mayr, *cristata* Mayr, *croesus* Emery, *froggatti* Forel, *impressa* (Mayr), *inornata* Crawley, *mayri* Emery, *metallica* (F. Smith), *tasmaniensis* Emery, *victoriae* Ern. André

5. Proceratiini

Discothyrea: *antarctica* Emery, 1 unidentified species
Proceratium: *croceum* (Roger), *silaceum* Roger, 1 unidentified species

6. Thaumatomyrmecini

Thaumatomyrmex: *mutilatus* Mayr

7. Ponerini

Belonopelta: *deletrix* Mann
Bothroponera: *cariosa* Emery, *denticulato* Kirby, *mayri* Emery, *piliventris* F. Smith, *porcata* Emery, *pumicosa* (Roger), *silvestrii* Santschi, *sjostedti* Mayr, *soror* (Emery), *sublaevis* Emery, 1 unidentified species
Brachyponera: *lutea* (Mayr), *sennaarensis* (Mayr)
Centromyrmex: *feae* Emery
Cryptopone: *gilva* (Roger), *mayri* Mann, *rotundiceps* Emery
Diacamma: *australe* (Fabricius), *rugosum* (Le Guillou), *scalpratum* (F. Smith)
Dinoponera: *grandis* (Guérin)
Euponera: *brunoi* Forel
Hagensia: *peringueyi* (Emery)
Hypoponera: *iheringi* (Forel), *nitidula* (Emery), *opaciceps* (Mayr), *opacior* (Forel), 1 unidentified species
Leptogenys: *consanguinea* W. M. Wheeler, *elongata* (Buckley), *fallax* (Mayr), *iheringi* Forel, *puncticeps* Emery, *turneri* Forel, 1 unidentified species
Megaponera:*foetens* (Fabricius)
Mesoponera: *australis* Forel, *caffraria* (F. Smith), *constricta* (Mayr), *fauveli* Emery, *gilberti* Kempf, *melanaria* (Emery), *pergandei* Forel, *rufonigra* Clark, *stigma* (Fabricius), *wroughtoni* Forel, 1 new species
Myopias: 1 unidentified species
Neoponera: *apicalis* (Latreille), *cavinodis* Mann, *crenata* (Roger), *moesta* (Mayr), *obscuricornis* Emery, *villosa* (Fabricius)
Odontoponera: *transversa* (F. Smith)
Ophthalmopone: *berthoudi* Forel
Pachycondyla: *crassinoda* (Latreille), *harpax* (Fabricius), *striata* F. Smith
Ponera: *leae* Forel, *pennsylvanica* Buckley
Psalidomyrmex: *procerus* Emery
Simopelta: *pergandei* Forel
Trapeziopelta: *tasmaniensis* (W. M. Wheeler), 1 unidentified species

8. Odontomachini

Anochetus: *emarginatus* (Fabricius), *graeffei* Mayr, *horridus* Kempf, *mayri* Emery, 2 unidentified species
Odontomachus: *biolleyi* Forel, *cephalotes* F. Smith, *chelifer* (Latreille), *haematoda* (Linnaeus), *hastatus* (Fabricius), *rixosus* F. Smith, *tyrannicus* F. Smith

PSEUDOMYRMECINAE

Pachysima: *aethiops* (F. Smith), *latifrons* Emery

Pseudomyrmex: *adustus* Borgmeier, *alliodorae* W. M. Wheeler, *apache* Creighton, *belti* Emery, *brunneus* F. Smith, *caroli* Forel, *championi* Forel, *decipiens* Forel, *elegans* F. Smith, *elongatus* Mayr, *filiformis* (Fabricius), *godmani* Forel, *gracilis* (Fabricius), *pallidus* F. Smith, *pazosi* Santschi, *rufomedius* F. Smith, *satanicus* W. M. Wheeler, *schuppi* Forel, *sericeus* Mayr, *subtilissimus* Emery, *termitarius* F. Smith, *triplarinus* (Weddell), 4 unidentified species

Tetraponera: *aitkeni* Forel, *allaborans* (Walker), *natalensis* F. Smith, 2 unidentified species

Viticicola: *tessmanni* (Stitz)

MYRMICINAE

1. Myrmicini

Hylomyrma: sp.

Manica: *bradleyi* (W. M. Wheeler), *hunteri* (W. M. Wheeler), *mutica* (Emery), *rubida* (Latreille)

Myrmica: *americana* Weber, *brevinodis* Emery, *brevispinosa* W. M. Wheeler, *emeryana* Forel, *lobicornis* Nylander, *monticola* W. M. Wheeler, *rubra* (Linnaeus), *smythiesi* Forel, *striologaster* Cole

Paramyrmica: *colax* Cole

Pogonomyrmex: *badius* (Latreille), *barbatus* (F. Smith), *occidentalis* (Cresson), *salinus* Olsen; (*Ephebomyrmex*) *huachucanus* W. M. Wheeler, *imberbiculus* W. M. Wheeler, *naegelii* Forel; (*Forelomyrmex*) *mayri* Forel

2. Pheidolini

Aphaenogaster: (*Attomyrma*) *famelica* (F. Smith), *flemingi* M. R. Smith, *floridana* M. R. Smith, *megommata* M. R. Smith, *rudis* Emery, *subterranea* (Latreille), *tennesseenis* (Mayr), *texana* Emery, *treatae* Forel, *uinta* W. M. Wheeler, 1 unidentified species; (*Deromyrma*) *araneoides* Emery, 2 unidentified species; (*Nystalomyrma*) *longiceps* (F. Smith), *pythia* Forel

Ischnomyrmex: *longipes* (F. Smith)

Machomyrma: *froggatti* Forel

Messor: *barbarus* (Linnaeus)

Novomessor: *albisetosus* (Mayr), *cockerelli* (Ern. André), *manni* (W. M. Wheeler & Creighton)

Pheidole: *brevicornis* Mayr, *californica* Mayr, *dentata* Mayr, *dentigula* M. R. Smith, *guilelmimuelleri* Forel, *hyatti* Emery, *megacephala* (Fabricius), *metallescens* Emery, *micula* W. M. Wheeler, *moerens* W. M. Wheeler, *morrisi* Forel, *nodus* F. Smith, *pilifera* (Roger), *tepicana* Pergande, *yaqui* Creighton & Gregg

Stenamma: *dieẞki* Emery, *manni* W. M. Wheeler, 1 unidentified species

Veromessor: *andrei* (Mayr), *chamberlini* (W. M. Wheeler), *lobognathus* (Andrews), *pergandei* (Mayr), *smithi* Cole

3. Melissotarsini

Rhopalomastrix: *rothneyi* Forel

6. Myrmicariini

Myrmicaria: *eumenoides* (Gerstaecker)

7. Cardiocondylini

Cardiocondyla: *elegans* Emery, *nuda* (Mayr)

8. Crematogastrini

Crematogaster: *auberti* Emery, *australis* Mayr, *cerasi* (Fitch), *clara* Mayr, *depilis* W. M. Wheeler, *lineolata* (Say), *menileki* Forel, *vermiculata* Emery; (*Apterocrema*) *titlanica* W. M. Wheeler; (*Eucrema*) *acuta* (Fabricius); (*Orthocrema*) *brevispinosa* Mayr, *limata* F. Smith, *minutissima* Mayr, *victima* F. Smith; (*Physocrema*) *deformis* F. Smith

9. Solenopsidini

Allomerus: *decemarticulatus* Mayr

Anergates: *atratulus* (Schenck)

Anergatides: *kohli* Wasmann

Chelaner: *antarcticus* (F. Smith)

Huberia: *striata* (F. Smith)

Liomyrmex: *aurianus* Emery

Megalomyrmex: *symmetochus* W. M. Wheeler

Monomorium: *ebeninum* Forel, *floricola* (Jerdon), *fultor* Forel, *ilia* Forel, *minimum* (Buckley), *pharaonis* (Linnaeus)
Oxyepoecus: 1 unidentified species
Solenopsis: *fugax* (Latreille), *geminata* (Fabricius), *globularia* (F. Smith), *molesta* (Say), *pergandei* Forel, *picea* Emery, *picta* Emery, *tenuis* Mayr, *texana* Emery, *xyloni* McCook
Tranopelta: *gilva* Mayr
Vollenhovia: *oblonga* (F. Smith), 1 unidentified species
Xenomyrmex: *stolli* Forel

10. Pheidologetini

Carebara: *lignata* Westwood, *winifredae* W. M. Wheeler, 1 unidentified species
Lophomyrmex: *quadrispinosus* (Jerdon)
Oligomyrmex: *corniger* Forel, *jacobsoni* Forel, *mjobergi* Forel, *parvicornis* Forel, *sundaicus* Forel
Paedalgus: *termitolestes* W. M. Wheeler
Pheidologeton: *affinis* (Jerdon), *diversus* (Jerdon)
Trigonogaster: *recurvispinosa* Forel

11. Myrmecinini

Dacryon: *rugosum* (Clark)
Dilobocondyla: *chapmani* W. M. Wheeler
Myrmecina: *americana* Emery, *australis* Forel
Podomyrma: *adelaidae* (F. Smith), 1 unidentified species
Pristomyrmex: *japonicus* Forel, *pungens* Mayr, *wheeleri* Taylor; (*Odontomyrmex*) *quadridentatus* Ern. André, 2 unidentified species

12. Meranoplini

Calyptomyrmex: *cataractae* Arnold
Mayriella: *abstinens* Forel
Meranoplus: *dimidiatus* F. Smith, *oceanicus* F. Smith, 1 unidentified species

13. Leptothoracini

Apsychomyrmex: *myops* W. M. Wheeler
Dacetinops: *cibdela* Brown & Wilson
Harpagoxenus: *americanus* Emery
Leptothorax: *ambiguus* Emery, *carinatus* Cole, *congruus* F. Smith, *hispidus* Cole, *longispinosus* Roger, *nevadensis* W. M. Wheeler, *nitens* Emery, *obturator* W. M. Wheeler, *rugatulus* Emery, *schaumi* Roger, *texanus* W. M. Wheeler, *tuberum* (Fabricius); (*Dichothorax*) *pergandei* Emery; (*Mychothorax*) *acervorum* (Fabricius), *canadensis* Provancher, *provancheri* Emery; (*Nesomyrmex*) *echinatinodis* Forel
Macromischa: *bermudezi* W. M. Wheeler, *manni* W. M. Wheeler, *wheeleri* Mann
Macromischoides: *aculeatus* (Mayr)
Rogeria: *procera* Emery, *stigmatica* Emery

14. Ocymyrmecini

Ocymyrmex: *arnoldi* Forel

15. Tetramoriini

Tetramorium: *caespitum* (Linnaeus), *guineense* (Fabricius), *striativentre* Mayr
Triglyphothrix: *striatidens* Emery
Xiphomyrmex: *turneri* Forel, 1 unidentified species

16. Ochetomyrmecini

Wasmannia: *auropunctata* (Roger)

17. Cataulacini

Cataulacus: *egenus* Santschi, *horridus* F. Smith, *taprobanae* F. Smith

18. Cryptocerini

Cephalotes: *atratus* (Linnaeus)
Cryptocerus: *maculatus* F. Smith, *minutus* Fabricius, *multispinus* Emery, *pallens* Klug, *pusillus* Klug, *umbraculatus* Fabricius, *varians* F. Smith, *wheeleri* Forel
Procryptocerus: *adlerzi* (Mayr), *pictipes* Emery, *regularis* Emery, *schmalzi* Emery, *striatus* (F. Smith)
Zacryptocerus: *clypeatus* (Fabricius)

19. Basicerotini

Aspididris: *militaris* Weber
Basiceros: 1 unidentified species

Eurhopalothrix: *australis* Brown & Kempf; *bolaui* (Mayr)
Rhopalothrix: *gravis* Mann

20. Dacetini

Acanthognathus: *rudis* Brown & Kempf
Alistruma: 1 unidentified species
Clarkistruma: *alinodis* (Forel)
Colobostruma: 1 unidentified species
Daceton: *armigerum* (Latreille)
Epopostruma: *alata* Forel, *frosti* (Brown), *quadrispinosa* (Forel), 3 unidentified species
Mesostruma: *browni* Taylor, *laevigata* Brown
Orectognathus: *antennatus* F. Smith, *clarki* Brown, *mjobergi* Forel, *nigriventris* Mercovich, *rostratus* Lowery, *satan* Brown, *versicolor* Donisthorpe
Smithistruma: *alberti* (Forel), *epinotalis* (Weber), *nigrescens* (W. M. Wheeler), *pergandei* (Emery), *rostrata* (Emery), *schulzi* (Emery), *studiosi* (Weber), *talpa* (Weber)
Strumigenys: *australis* Forel, *biolleyi* Forel, *decollata* Mann, *elongata* Roger, *godmani* Forel, *lewisi* Cameron, *louisianae* Roger, *micretis* Brown, *nidifex* Mann, *perplexa* (F. Smith), *saliens* Mayr, 1 unidentified species

25. Attini

Acromyrmex: *emilii* Forel, *lundi* Guérin, *octospinosus* (Reich)
Apterostigma: *collare* Emery, *mayri* Forel, *tramitis* Weber
Atta: *cephalotes* (Linnaeus), *columbica* Guérin, *sexdens* (Linnaeus), *texana* (Buckley)
Cyphomyrmex: *costatus* Mann, *olitor* Forel, *rimosus* (Spinola), *strigatus* Mayr
Mycetosoritis: *hartmanni* W. M. Wheeler
Myrmicocrypta: *spinosa* Weber, *urichi* Weber
Sericomyrmex: *amabilis* W. M. Wheeler
Trachymyrmex: *diversus* Mann, *jamaicensis* Ern. André, *septentrionalis* McCook, *wheeleri* (Weber)

ANEURETINAE

Aneuretus: *simoni* Emery

DOLICHODERINAE

1. Dolichoderini

Dolichoderus: *attelaboides* (Fabricius), *decollatus* F. Smith; (*Acanthoclinea*) *clarki* W. M. Wheeler; (*Hypoclinea*) *australis* Ern. André, *bidens* (Linnaeus), *bitubercalatus* (Mayr), *championi* Forel, *germaini* Emery, *mariae* Forel, *plagiatus* (Mayr), *pustulatus* Mayr, *scabridus* Roger, *taschenbergi* Mayr; (*Monacis*) *bispinosus* Olivier, *debilis* Emery, *laminatus* (Mayr)

2. Leptomyrmecini

Leptomyrmex: *erythrocephalus* (Fabricius), *nigriventris* (Guérin), *pictus* W. M. Wheeler, *unicolor* Emery, *varians* Emery

3. Tapinomini

Araucomyrmex: *tener* (Mayr)
Azteca: *alfari* Emery, *instabilis* (F. Smith), *longiceps* Emery, *xanthochroa* (Roger)
Bothriomyrmex: *inquilinus* Santschi, *meridionalis* (Roger), *pusillus* (Mayr)
Dorymyrmex: *pyramicus* (Roger) [Now called *Conomyrma insana* (Buckley).]
Engramma: *lujae* Forel
Forelius: *brasiliensis* (Forel), *foetidus* (Buckley)
Froggattella: *kirbyi* (Lowne)
Iridomyrmex: *conifer* Forel, *detectus* (F. Smith), *glaber* Mayr, *gracilis* Lowne, *itinerans* Lowne, *itoi* Forel, *melleus* W. M. Wheeler, *nitidus* Mayr, *pruinosus* (Roger), *punctatissimus* Emery, *viridiaeneus* Viehmeyer
Liometopum: *apiculatum* Mayr
Tapinoma: *luteum* Emery, *melanocephalum* (Fabricius), *sessile* (Say)
Technomyrmex: *albipes* F. Smith, *gibbosus* W. M. Wheeler, 2 unidentified species

FORMICINAE

3. Melophorini

Diodontolepis: *spinisquamis* Ern. André
Melophorus: *bagoti* Lubbock, *turneri* Forel

Notoncus: ***ectatommoides*** Forel, ***enormis*** Szabó, ***foreli*** Ern. André
Prolasius: 1 unidentified species

4. Formicini

Acanthomyops: ***claviger*** (Roger), ***coloradensis*** (W. M. Wheeler), ***mexicanus*** (W. M. Wheeler), ***subglaber*** (Emery)
Formica: ***altipetens*** W. M. Wheeler, ***bradleyi*** W. M. Wheeler, ***cinerea*** Mayr, ***fusca*** Linnaeus, ***neoclara*** Emery, ***neogagates*** Emery, ***neorufibarbis*** Emery, ***obscuripes*** Forel, ***pallidefulva*** Latreille, ***ulkei*** Emery; ***(Raptiformica) subnuda*** Emery
Lasius: ***alienus*** (Foerster), ***neoniger*** Emery, ***sitkaensis*** Pergande; ***(Cautolasius) flavus*** (Fabricius); ***(Chthonolasius) minutus*** Emery, ***umbratus*** (Nylander)
Myrmecocystus: ***kennedyi*** Cole, ***lugubris*** W. M. Wheeler, ***melliger*** Forel, ***mexicanus*** Wesmael, ***mimicus*** W. M. Wheeler, ***testaceus*** Emery
Polyergus: ***breviceps*** Emery, ***lucidus*** Mayr

5. Gesomyrmecini

Gesomyrmex: ***kalshoveni*** W. M. Wheeler, ***luzonensis*** W. M. Wheeler

6. Gigantiopini

Gigantiops: ***destructor*** (Fabricius)

7. Oecophyllini

Oecophylla: ***longinoda*** (Latreille), ***smaragdina*** (Fabricius)

8. Myrmecorhynchini

Myrmecorhynchus: ***carteri*** Clark, ***emeryi*** Ern. André

9. Plagiolepidini

Acropyga: ***australis*** Forel, ***moluccana*** Mayr
Plagiolepis: ***(Anoplolepis) custodiens*** (F. Smith), ***longipes*** (Jerdon)

10. Brachymyrmecini

Brachymyrmex: ***depilis*** Emery
Prenolepis: ***imparis*** (Say)
Stigmacros: ***acuta*** McAreavey, ***anthracina*** McAreavey, ***barretti*** Santschi, 1 unidentified species

11. Myrmelachistini

Myrmelachista: ***ambigua*** Forel, ***zeledoni*** Emery
Paratrechina: ***bruesi*** (W. M. Wheeler), ***melanderi*** (W. M. Wheeler), ***parvula*** (Mayr)

12. Camponotini

Calomyrmex: ***albopilosus*** (Mayr), ***impavidus*** (Forel)
Camponotus: ***americanus*** Mayr, ***herculeanus*** (Linnaeus), ***laevigatus*** (F. Smith), ***noveboracensis*** (Fitch), ***pennsylvanicus*** (DeGeer); ***(Colobopsis) culmicola*** W. M. Wheeler, ***etiolatus*** W. M. Wheeler, ***fictor*** Forel, ***gasseri*** Forel, ***mississippiensis*** M. R. Smith; ***(Dinomyrmex) famelicus*** Emery, 1 unidentified species; ***(Myrmamblys) vivdus*** (F. Smith); ***(Myrmaphaenus) fastigatus*** Roger, ***novogranadensis*** Mayr, ***yogi*** W. M. Wheeler; ***(Myrmentoma) anthrax*** W. M. Wheeler, ***nearcticus*** Emery; ***(Myrmeurynota) linnaei*** Forel; ***(Myrmobrachys) brevis*** Forel, ***canescens*** Santschi, ***planatus*** Roger, ***zoc*** Forel; ***(Myrmocladoecus) latangulus*** Roger; ***(Myrmogonia) tristis*** Clark; ***(Myrmophyma) adami*** Forel, ***aeneopilosus*** Mayr, ***arcuatus*** Mayr, ***capito*** Mayr, ***ceriseipes*** Clark, ***evae*** Forel, ***ephippium*** (F. Smith), ***eremicus*** W. M. Wheeler, ***froggatti*** Forel, ***hartogi*** Forel, ***innexus*** Forel, ***insipidus*** Forel, ***nigroaeneus*** (F. Smith); ***(Myrmosaulus) intrepidus*** (Kirby), ***molossus*** Forel, ***suffusus*** (F. Smith); ***(Myrmosphincta) sexguttatus*** (Fabricius); ***(Myrmothrix) abdominalis*** (Fabricius); ***(Myrmotrema) foraminosus*** Forel; ***(Orthonotomyrmex)*** 1 unidentifed species; ***(Pseudocolobopsis) alboannulatus*** Mayr, ***claviscapus*** Forel, ***pallescens*** Mayr, ***ustus*** Forel; ***(Tanaemyrmex) festinatus*** (Buckley), ***humilior*** Forel, ***nigriceps*** (F. Smith), ***ocreatus*** Emery, ***postcornutus*** Clark, ***sansabeanus*** (Buckley), ***santosi*** Forel, ***simillimus*** (F. Smith), ***vicinus*** Mayr
Dendromyrmex: ***fabricii*** (Roger)
Echinopla: 1 unidentified species
Opisthopsis: ***haddoni*** Emery, ***rufithorax*** Emery, ***rufoniger*** Forel
Polyrhachis: ***lamellidens*** F. Smith; ***(Campomyrma) femorata*** F. Smith, ***hecuba*** Forel, ***schwiedlandi*** Forel, 1 unidentified species; ***(Chariomyrma) hookeri*** Lowne; ***(Hagiomyrma) schencki*** Forel; ***(Hedomyrma) chrysothorax*** Viehmeyer, ***turneri*** Forel. 1 unidentified species; ***(Myrma) gagates*** F. Smith, ***laboriosa*** F. Smith, ***militaris*** (Fabricius); ***(Myrmatopa)*** 1 unidentified species; ***(Myrmhopla) dives*** F. Smith, ***hippomanes*** F. Smith, ***simplex*** Mayr, ***wheeleri*** Mann

C. ENEMIES OF ANT LARVAE

PHYLUM PLATYHELMINTHES

Raillietina spp. (poultry tapeworm). Ants may become infested in the larval stage. *Tetramorium.*

PHYLUM NEMATODA

Mermis spp., *Pelodera janeti, Allomermis myrmecophila.* Ants presumably become infested by worm larvae in the larval stage; infested adult ants are termed mermithogynes. *Aphaenogaster, Camponotus, Ectatomma, Formica, Lasius, Leptothorax, Myrmica, Neoponera, Odontomachus, Pachycondyla, Paraponera, Plagiolepis, Solenopsis.*

PHYLUM ARTHROPODA
CLASS ARACHNIDA

Spider. Predation. *Megaponera.*
Mite (*Pigmephorus* sp.) *Proceratium.*

CLASS INSECTA
ORDER COLEOPTERA

CARABIDAE: *Helluomorphoides latitarsis, H. ferrugineus.* Predation. *Neivamyrmex. Pseudomorpha laevissima.* Predation. *Camponotus. Tachyura incurva.* Predation. *Formica.*

CHRYSOMELIDAE: *Clytra quadripunctata.* Predation. *Formica.*

CLAVIGERIDAE: *Adranes lecontei, Claviger testaceus.* Predation. *Lasius.*

HISTERIDAE: *Haeterius ferrugineus, Myrmetes piceus.* Predation. *Formica, Lasius.*

PSELAPHIDAE: *Batrisodes delaportei, Ceophyllus monilis, Tmesiphorus costalis.* Predation. *Aphaenogaster, Lasius.*

SCARABAEIDAE: *Cremastocheilus armatus, C. stathamae.* Predation. *Formica, Myrmecocystus.*

STAPHYLINIDAE: *Atemeles spp., Dinarda dentata, Euryusa sinuata, Homoeusa acuminata, Lamprinus* spp., *Lomechusa strumosa, Myrmedonia limbata, Xenodusa cava,* undetermined staphylinid. Predation. *Atta, Formica, Lasius.*

ORDER LEPIDOPTERA

CYCLOTORNIDAE: *Cyclotorna monocentra.* Predation. *Iridomyrmex.*

LYCAENIDAE: *Lycaena arion, Liphyra brassolis.* Predation. *Myrmica, Oecophylla.*

ORDER DIPTERA

MUSCIDAE: *Bengalia* spp., *Ochromyia* sp. Predation. *Monomorium.*

PHORIDAE: *Metopina pachycondylae.* Social parasite (or commensal?). Undetermined phorid. *Pachycondyla, Formica, Gnamptogenys.*

SYRPHIDAE: *Microdon balipterus.* Predation. *Monomorium.*

FAMILY INDET.: Parasitism. *Dolichoderus, Technomyrmex.*

ORDER HYMENOPTERA

EUCHARITIDAE: *Chalcura bedeli, Ch.* sp.; *Chalcuroides versicolor; Eucharis ascendens, E. bedeli, E. myrmeciae, E. scutellaris; Eucharomorpha wheeleri; Isomerala coronata; Kapala cuprea, K. floridana, K. terminalis, K.* sp.; *Orasema argentina, O. coloradensis, O. constaricensis, O. duellojuradoi, O. minutissima, O. pheidolophaga, O. robertsoni, O. sixaolae, O. tolteca, O. viridis, O. wheeleri; Pseudochalcura gibbosa; Pseudometagea schwarzi; Psilogaster fasciiventris, Ps. fraudulentus; Rhipipallus affinis; Schizaspidia calomyrmecis, S. convergens, S. doddi, S. polyrhachicida, S. tenuicornis; Stilbula cynipiformis, S. tenuicornis; Thoracantha bruchi; Tricoryna chalcoponerae, T. ectatommae.* HOST GENERA: *Calomyrmex, Camponotus, Cataglyphis, Ectatomma, Formica, Lasius, Myrmecia, Odontomachus, Pachycondyla, Pheidole, Pogonomyrmex, Polyrhachis, Rhytidoponera, Solenopsis, Wasmannia.*

EULOPHIDAE: *Melittobia acosta.* Experimental. *Formica, Lasius.*

ICHNEUMONIDAE: *Pezomachus sericeus.* Experimental. *Camponotus.*

PROCTOTRUPIDAE: *Tetramopria donisthorpei, T. femoralis.* Probably parasitism. *Tetramorium.*

FORMICIDAE: *Formica (Raptiformica)* spp., *Harpagoxenus sublaevis, Polyergus* spp. Predaceous. *Formica, Leptothorax.* Thief ants, *Solenopsis* spp., feed on the brood of many genera of ants. All army ants (subfamily Dorylinae) include among their prey the brood of other ants.

PHYLUM VERTEBRATA
CLASS REPTILIA

Typhlops punctatus (blind-snake). Bequaert (1930: 167) found a snake in Liberia "literally stuffed with thousands of larvae and pupae of a small ant. Only a few workers were mixed with them and no other kind of food was present."

CLASS MAMMALIA

Any mammal that is capable of digging up or breaking open formicaries is a potential enemy of ant larvae, since these predators undoubtedly consume all stages indiscriminately. Direct evidence, however, is meager.

ORDER CARNIVORA

URSIDAE: *Ursus americanus* (black bear). Predation. *Camponotus,* etc.

ORDER PHOLIDOTA

MANIDAE: *Manis javanica* (scaly anteater). Predation.

ORDER PRIMATES

HOMINIDAE: *Homo sapiens.* Predation; reported eaten in Australia, Burma, California (Digger Indians), China, India, Japan, Siam, etc. *Camponotus, Oecophylla;* usually the genus was not mentioned.

ORDER XENARTHRA

MYRMECOPHAGIDAE: *Cyclopes* spp., *Myrmecophaga* spp., *Tamandua* spp. Predation.

D. CHARACTERS OF ANT LARVAE AND THEIR VALUE AS USED IN COMPUTING THE SPECIALIZATION INDICES

BODY—Shape: pogonomyrmecoid 0; aphaenogastroid, myrmecioid, pheidoloid 1; dolichoderoid, leptanilloid, platythyreoid 2; attoid, crematogastroid, leptomyrmecoid, oecophylloid, rhopalomastigoid 3. Spiracles: 10 pairs, equal in size, not on papillae 0; on papillae, or metathoracic or AI largest, others smaller 1; eight or nine pairs 2; one pair 3. Spinules: present 0; absent 1. Protuberances: lacking 0; present 1. Anus: ventral or posteroventral and without lips 0; posterior, or with lips 1.

BODY HAIRS—Abundance: few to numerous 0; naked, nearly naked or dense 1. Variety: one type per genus 0; more 1. Shape: unbranched and smooth—slightly curved or straight 0, spinelike 1, flexible 1, uncinate 2, anchor-tipped 3; unbranched and denticulate—denticulate throughout most of length 1, flexible and denticulate throughout 1, denticulate on distal half 1, tip denticulate 1, flagelliform with denticulate base 2, uncinate and denticulate 2, flattened distally and with denticulate margin 2; bifid and smooth—tip bifid 1, half-bifid 1, deeply bifid with curled tips 2, deeply bifid with long flexible branches 2; bifid and partly denticulate—tip bifid and denticulate 1, half bifid and branches denticulate 1; multifid and smooth—branches short 1, branches long and flexible 1, branching dichotomously 1, branching dendritically 2; miscellaneous —7 shapes at 2 each.

HEAD—Shape: subhexagonal 0, other 1. Proportions: wider than long 0, other 1. Spinules: none 0, present 1.

HEAD HAIRS—Abundance: 40 or fewer 0, numerous or none 1. Shape: unbranched, smooth, straight or slightly curved 0, other 1. Variety: only one shape 0, other 1. Comparison with body hairs: differing in abundance, size and shape 0, other 1.

ANTENNAE—Position: at or above middle 0, below middle 1. Size: medium 0, large or small 1. Number of sensilla: three 0, other 1.

LABRUM—Size: medium 0, small or large 1. Proportions: breadth = twice the length 0, other 1. Shape: bilobed 0, other 1. Spinules on posterior surface: numerous 0, few 1, none 2. Sensilla: ten or fewer 0, more than ten 1, none 1.

MANDIBLES—Size: medium 0, large or small 1. Proportions: medium 0, stout or

slender 1. Sclerotization: medium 0, feeble or heavy 1. Shape: ectatommoid 0; pogonomyrmecoid, amblyoponoid, pristomyrmecoid, pheidoloid, platythyreoid and dinoponeroid 1; cephalotoid, attoid, diacammoid, tetraponeroid, rhytidoponeroid, camponotoid, dolichoderoid and typhlomyrmecoid 2; leptanilloid, anergatidoid and leptogenyoid 3. Spinules on anterior and/or posterior surfaces: none 0, present 1.

MAXILLAE—Shape: conoidal or paraboloidal 0, other 1. Spinules: present 0, none 1. Palp: paxilliform 0, other shapes 1; five sensilla 0, other numbers 1. Galea: digitiform 0, other shapes 1; two sensilla 0, other numbers 1.

LABIUM—Spinules: numerous 0, sparse 1, none 2; arranged in rows 0, isolated 1. Palp: paxilliform or papilliform 0, other shapes 1, none 2; five sensilla 0, other numbers 1. Opening of sericteries: a transverse slit 0, other shapes 1.

HYPOPHARYNX—Spinules numerous 0, sparse 1, none 2; minute 0, large 1; arranged in rows 0, isolated 1.

CHILOSCLERES—None 0, present 1.

PRAESAEPIUM—None 0, present 1.

TROPHOTHYLAX—None 0, present 2.

E. SPECIALIZATION INDICES[3]

FAMILY FORMICIDAE 22

SUBFAMILY DORYLINAE 24

Aenictus 23, *Cheliomyrmex* 25, *Dorylus* 28, *Eciton* 21, *Labidus* 22, *Neivamyrmex* 27.

SUBFAMILY LEPTANILLINAE 35

Leptanilla 38, *Leptomesites* 33.

SUBFAMILY CERAPACHYINAE 21

Cerapachys 23, *Eusphinctus* 24, *Lioponera* 22, *Phyracaces* 16.

SUBFAMILY MYRMECIINAE 23

Myrmecia 23.

SUBFAMILY PONERINAE 17

TRIBE AMBLYOPONINI 17: *Ambloyopone* 18, *Apomyrma* 22, *Myopopone* 17, *Onychomyrmex* 19, *Prionopelta* 11, *Stigmatomma* 14.

TRIBE PLATYTHYREINI 20: *Eubothroponera* 20, *Plathythyrea* 20.

TRIBE TYPHLOMYRMECINI 15: *Typhlomyrmex* 15.

TRIBE ECTATOMMINI 15: *Ectatomma* 14, *Gnamptogenys* 14, *Heteroponera* 11, *Paraponera* 12, *Rhytidoponera* 21.

TRIBE PROCERATIINI 31: *Discothyrea* 32, *Proceratium* 31.

TRIBE PONERINI 17: *Belonopelta* 16, *Bothroponera* 19, *Brachyponera* 16, *Centromyrmex* 16, *Cryptopone* 14, *Diacamma* 16, *Dinoponera* 19, *Euponera* 16, *Hagensia* 18, *Hypoponera* 13, *Leptogenys* 23, *Megaponera* 17, *Mesoponera* 15, *Myopias* 21, *Neoponera* 17, *Odontoponera* 18, *Ophthalmopone* 19, *Pachycondyla* 15, *Ponera* 13, *Psalidomyrmex* 17, *Trapeziopelta* 18.

TRIBE ODONTOMACHINI 19: *Anochetus* 20, *Odontomachus* 18.

SUBFAMILY PSEUDOMYRMECINAE 26

Pachysima 26, *Pseudomyrmex* 26, *Tetraponera* 28, *Viticicola* 24.

SUBFAMILY MYRMICINAE 20

TRIBE MYRMICINI 16: *Manica* 17, *Myrmica* 18, *Paramyrmica* 14, *Pogonomyrmex* 17.

TRIBE PHEIDOLINI 13: *Aphaenogaster* 14, *Ischnomyrmex* 12, *Machomyrma* 16, *Messor* 14, *Novomessor* 14, *Pheidole* 14, *Stenamma* 12, *Veromessor* 11.

TRIBE MELISSOTARSINI 31: *Rhopalomastix* 31.

TRIBE MYRMICARIINI 21: *Myrmicaria* 21.

TRIBE CARDIOCONDYLINI 17: *Cardiocondyla* 17.

TRIBE CREMATOGASTRINI 35: *Crematogaster* 35.

TRIBE SOLENOPSIDINI 20: *Allomerus* 25, *Anergates* 30, *Chelaner* 18, *Liomyr-*

[3] All figures rounded to whole numbers.

mex 19, *Megalomyrmex* 18, *Monomorium* 23, *Oxyepoecus* 15, *Solenopsis* 17, *Vollenhovia* 17, *Xenomyrmex* 25.

TRIBE PHEIDOLOGETINI 20: *Carebara* 24, *Lophomyrmex* 14, *Oligomyrmex* 28, *Paedalgus* 23, *Pheidologeton* 21, *Trigonogaster* 14.

TRIBE MYRMECININI 22: *Dacryon* 21, *Dilobocondyla* 27, *Myrmecina* 23, *Podomyrma* 21, *Pristomyrmex* 17.

TRIBE MERANOPLINI 18: *Calyptomyrmex* 17, *Mayriella* 24, *Meranoplus* 13.

TRIBE LEPTOTHORACINI 23: *Leptothorax* 27, *Macromischa* 26, *Macromischoides* 17, *Rogeria* 22.

TRIBE OCYMYRMECINI 16: *Ocymyrmex* 16.

TRIBE TETRAMORIINI 13: *Tetramorium* 13.

TRIBE OCHETOMYRMECINI 18: *Wasmannia* 18.

TRIBE CATAULACINI 28: *Cataulacus* 28.

TRIBE CRYPTOCERINI 26: *Cephalotes* 25, *Cryptocerus* 24, *Procryptocerus* 28.

TRIBE BASICEROTINI 16: *Aspididris* 16, *Basiceros* 19, *Eurhopalothrix* 12, *Rhopalothrix* 16.

TRIBE DACETINI 15: *Acanthognathus* 16, *Alistruma* 18, *Clarkistruma* 12, *Colobostruma* 13, *Daceton* 20, *Epopostruma* 13, *Mesostruma* 15, *Orectognathus* 13, *Smithistruma* 15, *Strumigenys* 14.

TRIBE ATTINI 27: *Acromyrmex* 28, *Apterostigma* 29, *Atta* 29, *Cyphomyrmex* 25, *Mycetosoritis* 20, *Myrmicocrypta* 28, *Sericomyrmex* 27, *Trachymyrmex* 28.

SUBFAMILY DOLICHODERINAE 24

Araucomyrmex 20, *Azteca* 23, *Bothriomyrmex* 24, *Dolichoderus* 25, *Dorymyrmex* 24, *Engramma* 27, *Forelius* 25, *Froggattella* 24, *Iridomyrmex* 25, *Leptomyrmex* 24, *Tapinoma* 29.

SUBFAMILY FORMICINAE 17

TRIBE MELOPHORINI 15: *Diodontolepis* 17, *Melophorus* 14, *Notoncus* 13, *Prolasius* 14.

TRIBE FORMICINI 14: *Acanthomyops* 14, *Formica* 14, *Lasius* 18, *Myrmecocystus* 14, *Polyergus* 14.

TRIBE GESOMYRMECINI 17: *Gesomyrmex* 17.

TRIBE GIGANTIOPINI 16: *Gigantiops* 16.

TRIBE OECOPHYLLINI 24: *Oecophylla* 24.

TRIBE MYRMECORHYNCHINI 15: *Myrmecorhynchus* 15.

TRIBE PLAGIOLEPIDINI 13: *Acropya* 12, *Plagiolepis* 13.

TRIBE BRACHYMYRMECINI 17: *Brachymyrmex* 23, *Prenolepis* 13, *Stigmacros* 15.

TRIBE MYRMELACHISTINI 17: *Myrmelachista* 18, *Paratrechina* 16.

TRIBE CAMPONOTINI 22: *Calomyrmex* 24, *Camponotus* 22, *Dendromyrmex* 20, *Echinopla* 23, *Opisthopsis* 21, *Polyrhachis* 23.

F. LITERATURE CITED

(Citations to our papers on ant larvae are arranged taxonomically in Appendix A and hence are not included here.)

ADLERZ, G. 1886. Myrmecologiska Studier. II. Svenska Myror och deras Lefnadsförhållanden. Bihang till K. Svenska vet.-Akad. Handl. 11: 1-329, 7 pl.

ALLEE, W. C., A. E. EMERSON, O. PARK, T. PARK and K. P. SCHMIDT. 1949. Principles of animal ecology. W. B. Saunders Co., Philadelphia. 837 p.

ATHIAS-HENRIOT, C. 1947. Recherches sur les larves de quelques fourmis d'Algérie. Bull. Biol. France Belgique 81: 247-272.

BERLESE, A. 1902. Osservazioni su fenomeni che avvengono durante la ninfosi degli insetti metabolici. Riv. Patologia Vegetale 9: 177-344.

BERLESE, A. 1925. Gli insetti. Vol. II. Società Editrice Libraria, Milano. 992 p.

BERNARD, F. 1948. Les insectes sociaux du Fezzân. Comportement et biogéographie. Inst. Rech. Sahariennes Univ. d'Alger. Mission Sci. du Fezzân 1944-1945. V. Zoologie (Arthropodes, 1): 86-201, 2 pl.

—— 1951. Super-famille des Formicoidea, p. 907-1119, 1258-1263, 1272-1275. *In* P. P. Grassé (ed.) Traité de Zoologie, Tome X, Fasc. II. Masson & Cie, Paris.

——— 1955. Morphologie et comportment des fourmis lestobiotiques du genre *Epixenus* Emery. Insectes Sociaux 2: 273-283.

BISCHOFF, H. 1927. Biologie der Hymenopteren. Julius Springer, Berlin. 598 p.

BROWN. W. L., Jr. 1949. Revision of the ant tribe Dacetini: IV. Some genera properly excluded from the Dacetini, with the establishment of the Basicerotini new tribe. Trans. Amer. Entomol. Soc. 75: 83-96.

——— 1954. Remarks on the internal phylogeny and subfamily classification of the family *Formicidae*. Insectes Sociaux 1: 21-31.

——— 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini. Bull. Mus. Comp. Zool. Harvard 118: 175-362.

——— 1960. Contributions toward a reclassification of the Formicidae. III. Tribe Amblyoponini. Bull. Mus. Comp. Zool. Harvard 122: 145-230.

——— 1963. Characters and synonymies among the genera of ants. Part III. Some members of the tribe Ponerini. Breviora Mus. Comp. Zool. Harvard No. 190: 10 p.

——— 1973. A comparison of the hylean and Congo-West African rain forest ant faunas, p. 161-185. *In* B. J. Meggers, E. S. Ayensu and W. D. Duckworth (ed.) Tropical Forest Ecosystems in Africa and South America. Smithsonian Inst. Press, Washington.

——— and E. O. WILSON. 1959. The evolution of the dacetine ants. Quart. Rev. Biol. 34: 278-294.

——— W. H. GOTWALD and J. LÉVIEUX. 1970. A new genus of ponerine ants from West Africa with ecological notes. Psyche 77: 259-275.

BRUES, C. T. 1919. The classification of insects based on the characters of the larvae and pupae. Biol. Bull. 37: 1-21.

BUCHSBAUM, R. 1948. Animals without backbones (rev. ed.). Univ. Chicago Press, Chicago. 405 p.

CLAUSEN, C. P. 1940. Entomophagous insects. McGraw-Hill, New York. 688 p.

COLE, A. C. 1968. *Pogonomyrmex* harvester ants. A study of the genus in North America. Univ. Tennessee Press, Knoxville. 222 p.

COMSTOCK, J. H. 1925. An introduction to entomology (2 ed.) Comstock Publ. Co., Ithaca. 1044 p.

CREIGHTON, W. S. 1950. The ants of North America. Bull. Mus. Comp. Zool. Harvard 104: 1-585, 57 pl.

DELAGE, Bernadette. 1968. Recherches sur les fourmis moissonneuses du Bassin Aquitain: éthologie. Physiologie de l'alimentation. Ann. Sci. Natur. Zool. Biol. Anim. (12) 10: 197-266.

DELAGE-DARCHEN, Bernadette. 1972. Le polymorphisme larvaire chez les fourmis *Nematocrema* d'Afrique. Insectes Sociaux 19: 259-277.

DONISTHORPE, H. St. J. K. 1927. British ants. (2 ed.) Geo. Routledge & Sons, London. 436 p.

EIDMANN, H. 1928. Zur Kenntnis der Biologie der Rossameise (*Camponotus herculeanus* L.). Z. Angew. Entomol. 14: 229-253, 9 fig.

EMERY, C. 1899. Intorno alle larve di alcune formiche. Mem. R. Accad. Sci. Ist. Bologna 8: 3-10, 2 pl.

——— 1904. Le affinitá del genere *Leptanilla* e i limiti delle Dorylinae. Arch. Zool. 2: 107-116.

——— 1911. Fam. Formicidae, subfam. Ponerinae. Genera Insectorum, Fasc. 118: 125 p., 3 pl.

——— 1912. Études sur les Myrmicinae. Ann. Soc. Entomol. Belgique 56: 94-105.

——— 1921/1922. Fam. Formicidae, subfam. Myrmicinae. Genera Insectorum, Fasc. 174: 397 p., 7 pl.

——— 1925. Fam. Formicidae, subfam. Formicinae. Genera Insectorum, Fasc. 183: 302 p., 4 pl.

ESCHERICH, K. 1917. Die Ameise. 2nd ed. Friedr. Vieweg und Sohn, Braunschweig. 348 p.

ETTERSHANK, G. 1966. A generic revision of the world Myrmicinae related to *Solenopsis* and *Pheidologeton*. Australian J. Zool. 14: 73-171.

EVANS, H. E. 1958. Studies of the larvae of digger wasps. Part IV: Astatinae, Larrinae, and Pemphredoninae. Trans. Amer. Entomol. Soc. 84: 109-139.

——— 1965. A description of the larva of *Methocha stygia* (Say), with notes on other Tiphiidae. Proc. Entomol. Soc. Washington 67: 88-95.

——— and C. S. LIN. 1956. Studies on the larvae of digger wasps. Part II: Nyssoninae. Trans. Amer. Entomol. Soc. 82: 35-66.
FOREL, A. 1911. Sur le genre *Metapone* n. g. noveau groupe des Formicides et sur quelques autres formes nouvelles. Rev. Suisse Zool. 19: 445-459.
——— 1922. Le monde social des fourmis du globe comparé à celui de l'homme. Tome III. Librairie Kundig: Genève. 227 p. (Translated C. K. Ogden. 1928. G. P. Putnam's Sons, Ltd., London & New York. 551 & 445 p.)
ISHAY, J., and R. IKAN. 1968. Glucogenesis in the oriental hornet *Vespa orientalis*. Ecology 49: 169-171.
JANET, C. 1892. Communication sur le mécanisme de la succion chez les hyménoptères, et sur les poils d'accrochage à ressort des larves des fourmis. Ann. Soc. Entomol. France 61: xcvii-xcviii.
——— 1904. Observations sur les fourmis. Ducourtieux et Gout, Limoges. 68 p., 7 pl.
KEMPF, W. W. 1959. A synopsis of the New World species belonging to the *Nesomyrmex*-group of the ant genus *Leptothorax* Mayr. Studia Entomol. (Rio de Janeiro) (n.s.) 2: 291-432.
——— and K. LENKO. 1968. Novas observações e estudos sobre *Gigantiops destructor* (Fabricius). Papéis Avulsos Zool. S. Paulo 22: 209-230.
LE MASNE, G. 1951. Échange de nourriture trophallaxie et transports mutuels chez les fourmis, p. 1104-1119. *In* P. P. Grassé. Traité de Zoologie, Tome X, Fasc. II. Masson & Cie, Paris.
——— 1953. Observations sur les relations entre le couvain et les adultes chez les fourmis. Ann. Sci. Nat. Zool. Biol. Anim. (11)15: 1-55.
MENOZZI, C. 1930. Formiche della Somalia italiana meridionale. Mem. Soc. Entomol. Ital. 9: 76-130, 3 pl.
MICHENER, C. D. 1953a. Life-history studies in insect systematics. Syst. Zool. 2: 112-118.
——— 1953b. Comparative morphological and systematic studies of bee larvae with a key to the families of hymenopterous larvae. Univ. Kansas Sci. Bull. 35: 987-1102.
MÜLLER, W. 1886. Beobachtungen an Wanderameisen (*Eciton hamatum* Fabr.). Kosmos 18: 81-93.
SCHNEIRLA, T. C. 1957. Theoretical consideration of cyclic processes in doryline ants. Proc. Amer. Phil. Soc. (Philadelphia) 101: 106-133.
SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York. 247 p.
SNODGRASS, R. E. 1935. Principles of insect morphology. McGraw-Hill, New York. 667 p.
——— 1960. Some words and their ways in entomology. Proc. Entomol Soc. Washington 62: 205-270.
SUDD, J. H. 1967. An introduction to the behavior of ants. St. Martin's Press, New York. 200 p.
TANQUARY, M. C. 1913. Biological and embryological studies on Formicidae. Bull. Illinois State Lab. Natur. Hist. 9: 417-479, 8 pl.
TAYLOR, R. W. 1965. A monographic revision of the rare tropicopolitan ant genus *Probolomyrmex* Mayr. Trans. R. Entomol. Soc. London 117: 345-365.
——— 1967. A monographic revision of the ant genus *Ponera* Latreille. Entomol. Dept., Bishop Mus. (Honolulu), Pacific Insects Mon. 13: 112 p.
VALENTINI, Suzanne. 1951. Sur l'adaptation des larves de Formicoidea. Ann. Sci. Nat., Zool. Sér. 11: 249-276.
WEBER, N. A. 1972. Gardening ants, the attines. Mem. Amer. Phil. Soc. (Philadelphia) 92: 146 p.
WENT, F. W., J. WHEELER and G. C. WHEELER. 1972. Feeding and digestion in some ants (*Veromessor* and *Manica*). BioScience 22: 82-88.
WHEELER, G. C., and E. W. WHEELER. 1937. New hymenopterous parasites of ants. Ann. Entomol. Soc. Amer. 30: 163-175.
——— and J. WHEELER. 1970. The natural history of *Manica*. J. Kansas Entomol. Soc. 43: 129-162.
WHEELER, W. M. 1900. A study of some Texan Ponerinae. Biol. Bull. 2: 1-31.
——— 1902. An American *Cerapachys*, with remarks on the affinities of the Cerapachyinae. Biol. Bull. 3: 181-191.
——— 1903. Some notes on the habits of *Cerapachys augustae*. Psyche 10: 205-209.

——— 1910.[4] Ants. Columbia Univ. Press, New York. 663 p.
——— 1914. The ants of the Baltic amber. Schr. Phys.-ökonom. Ges. Königsberg 55: 1-142.
——— 1918. A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. Proc. Amer. Phil. Soc. (Philadelphia) 57: 293-343.
——— 1919. The ants of the genus *Metapone* Forel. Ann. Entomol. Soc. Amer. 12: 173-191.
——— 1920. The subfamilies of Formicidae, and other taxonomic notes. Psyche 27: 46-55.
——— 1922. The ants collected by the American Museum Congo Expedition. Bull. Amer. Mus. Natur. Hist. 45: 39-269, 21 pl.
——— 1923. Social life among the insects. Harcourt, Brace & Co., New York. 375 p.
——— 1926. Les sociétés d'insectes: leur origine—leur évolution. Gaston Doin et Cie., Paris. 468 p.
——— 1928. The social insects: their origin and evolution. Harcourt, Brace & Co., New York. 378 p.
——— and I. W. BAILEY. 1920. The feeding habits of pseudomyrmine and other ants. Trans. Amer. Phil. Soc. (Philadelphia) (Art. 4): 235-279, 5 pl.
WILSON, E. O. 1971. The insect societies. Harvard Univ. Press, Cambridge. 548 p.
——— F. M. CARPENTER and W. L. BROWN, Jr. 1967. The first Mesozoic ants. Science 157: 1038-1040.
——— T. EISNER, G. C. WHEELER and J. WHEELER. 1956. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. Comp. Zool. Harvard 115: 81-99.
——— and R. W. TAYLOR. 1964. A fossil ant colony: new evidence of social antiquity. Psyche 71: 93-103.

[4] This reference is often cited as 1926. I (G. C. W.) asked Dr. W. M. Wheeler in 1926 whether there had been any changes in the book since the first printing. His reply: No. The date therefore should be 1910, not a reprint date.